THE

PROCEEDINGS

OF THE

ROYAL

ENTOMOLOGICAL SOCIETY

OF

LONDON

Series A

GENERAL ENTOMOLOGY

VOL. 32

LONDON :

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W. 7

1957

PRINTED IN GREAT BRITAIN BY
ADLARD AND SON LIMITED
BARTHOLOMEW PRESS
DORKING SURREY

CONTENTS

ON THE HABITAT AND GROWTH STAGES OF *ARIXENIA ESAU* JORDAN AND *A. JACOBSONI* BURR (DERMAPTERA: ARIXENIOIDEA), WITH DESCRIPTIONS OF THE HITHERTO UNKNOWN ADULTS OF THE FORMER.

By J. L. Cloudsley-Thompson.

(*Department of Zoology, King's College, University of London.*)

Introduction.

The super-family Arixenioidea Chopard[1] is represented by two species, *Arixenia esau* Jordan and *A. jacobsoni* Burr, both of which are parasitic on bats in the Malay Peninsula and the East Indies. *A. esau* is known from four nymphs found by a London taxidermist in about 1909 in the breast pouch of a specimen of the Hairless Bulldog Bat (*Cheiromeles torquatus* Horsf.) (Jordan, 1909). A number of specimens of *A. jacobsoni* were obtained two years later from a cave inhabited by bats near Babakan, southern Java (Burr, 1912).

With the exception of the collection to be described below, no further specimens of *A. esau* appear to have been found since, but *A. jacobsoni* has occasionally been taken. Mr. R. A. Lever, Senior Entomologist to the Department of Agriculture, Federation of Malaya, writes that two or three specimens were collected from a Free-tailed Bat (*Tardaridus* (*Mops*) *mops* (de Blainv.)) in Kuala Lumpur on 3rd July, 1919. Two of these are preserved dry at the British Museum (Natural History). The British Museum collection also contains about 17 nymphs and 4 adults pinned and dry, collected by Dr. E. H. Taylor at Mindinao, Philippines, in 1912, as well as seven specimens taken from *T. mops* in Malaya by Dr. H. P. Hacker in 1920. These I have been able to examine by courtesy of the former Keeper, Mr. N. D. Riley, C.B.E., and Dr. D. R. Ragge. In addition I am grateful to Professor J. Bequaert and Dr. W. L. Brown, Assistant Curator in the Department of Insects, Museum of Comparative Zoology at Harvard College, Cambridge, Mass., U.S.A., for the loan of 35 specimens preserved in alcohol and labelled " South Java (Banjoemas) III. Cave near Babakan K.W.D. 1933 ".

Collection of *Arixenia* from Malaya, 1952.

The collection on which the present paper is mostly based was kindly given to me by Dr. J. R. Audy, Colonial Office Research Unit, Institute for Medical Research, Kuala Lumpur, Malaya, who has also supplied the following information. The specimens were taken from 18 Hairless Bulldog Bats (*Cheiromeles torquatus* Horsf.) (Nos. R.17558–75) from Dusun Wam, Bukit Lagong Forest Reserve, near Kepong, Selangor, Malaya (3° 14′ N., 101° 37′ E.) on 10th March, 1952, and from scrapings of guano, etc., from a hollow tree which harboured the bat colony on 14th March, 1952. They have been referred to by J. R. Audy (1952, *Bull. Raffles Mus.* **24** : 133*n*) and by J. L. Harrison (1954, *Malay. Nat. J.*

[1] Chopard (1949, fig. 398) gives an illustration labelled " *Arixenia jacobsoni* Burr " which is clearly a drawing of a nymph of *A. esau*.

9 : 67) and were exhibited at a meeting of the Royal Entomological Society in 1955 (Cloudsley-Thompson, J. L., 1955, *Proc. R. ent. Soc. Lond.* (C) **20** : 16). The locality in which they were taken is discussed and mapped by J. R. Audy (1954, *Malaysian Parasites*, I–XV : 6–7 Kuala Lumpur).

Dusun Wam is a fairly remote and tiny (3–4 huts) forest settlement of aborigines (Jakun) on a hillside about 1400 ft. altitude in the Bukit Lagong Forest Reserve some 10 air-miles NW. of Kuala Lumpur (Bukit = hill ; dusun = " orchard " or native plantation of a few fruit trees). This group of Jakun have collected for the Colonial Office Research Unit for many years. The following details have been recounted by the senior Dyak collector, Mr. Ben Ensoll :

" A large durian fruit tree (perhaps 4–5 ft. in diameter, near base) in the *dusun* had a hole some 40 ft. up the trunk where a branch had fallen off, and a colony of *Cheiromeles* had sheltered in this hollow for many years. The aborigines would periodically collect some of these bats for eating by fishing for them with the long extended raphes of rattan palms which have strong recurved thorns (because of the great difficulty of extracting oneself from their clutches, these and similar tentacles are often known as ' lawyer-vines ' in the tropics). Several of these would be pushed into the tree-hole with the aid of a pole and then pulled out, often with protesting bats firmly hooked to them. In due course the hollow tree died and, probably fearing the tree would fall down in their absence and that they would lose their bats, the aborigines blocked up the hole during the day and felled the tree. As Harrison (*loc. cit.*) says, ' According to their own account they caught three baskets full of bats, and many escaped. From the size of the baskets, they must have caught several hundred, perhaps six to eight hundred even, and the tree itself must have contained close on a thousand. Unfortunately I saw only a few bats, because most of them had been eaten. They were reported as very good '."

Nineteen of these bats were delivered to the laboratory of the Colonial Office Research Unit in rat-traps, often two or three bats per trap. One bat, without *Arixenia*, was kept alive under observation ; the remaining 18 were killed. A number of these bore a total of 17 specimens of *Arixenia*. Four other specimens of *Cheiromeles* and nine of the Wrinkled-lipped Bat (*Chaerephon jokhorensis* Dobson), also from hollow trees, have been received, but no other specimens of *Arixenia* have been seen. Indeed, apart from trombiculid mites, no ectoparasites were found.

Some of the specimens on the bats were over an inch long ; they were extremely active and moved quickly when they had to. While a bat was climbing about in a cramped wire-mesh rat-trap, it would repeatedly appear to be pinning an *Arixenia* against the wire, but the *Arixenia* would always slide quickly out of the way. One or two, which became detached, clung to Dr. Audy's clothes and gave a definite impression of being extremely adroit creatures which could not easily be knocked or brushed off. They wandered about mostly on the body of the bat but occasionally on its wings. No specimens were found in the peculiar gular " pouch " of the bats, although it was at first thought that these creatures might feed on the caseous material in these pouches, which is, of course, a possibility. The bat itself is hairless with a coarse, sooty skin and a strong goat-like smell. The " pouch " is a gular fold of the skin with a number of fairly strong hairs along its lips.

Cheiromeles also has subaxillary wing pouches into which it tucks the ends of its wings and then becomes adept at scrambling. Instructions were sent to the Jakun collectors to obtain quantities of guano and as many specimens of *Arixenia* as possible from the hollow tree : they were given bags for this purpose. This yielded a further 187 specimens which were also given to me by Dr. Audy, as well as one or two that he kept and some damaged fragments.

The 17 specimens actually taken from the bats, as well as 168 from the hollow tree, were found to be *A. esau*, while the remaining 19 specimens were identified as *A. jacobsoni*. Although a number have been dissected, preservation is not sufficiently good to permit anything being added to what is already known of the anatomy of *Arixenia* (Burr and Jordan, 1912). Nor could any recognisable matter be found in the contents of the crop.

The Growth Stages.

It has been established that the common earwig (*Forficula auricularia* L.) has five instars, four nymphal and one adult (Henson, 1947), while the New Zealand species *Anisolabis littorea* (White) has five nymphal instars, none of which exhibit external sexual dimorphism (Giles, 1952). Owing to the telescopic nature of the abdomen, body length is not a reliable measurement for developmental studies in the Dermaptera, and the growth of the head capsule and antennae are generally considered to be more reliable diagnostic features.

The head widths, taken at the broadest part behind the eyes, of the specimens of *Arixenia esau* and *A. jacobsoni* obtained from Malaya in 1952, and of the latter species from Java, 1933, are given in Table I, from which it can be seen that there is some overlap in size between the different instars. Figure 1 shows camera lucida drawings of the heads of typical specimens of the different instars indicating the change of shape that occurs with each moult. The material comprises four nymphal and the two adult stadia. The smallest nymphs are so large and heavily chitinised that I feel convinced that they must represent the second instar even if, as seems probable, both species are ovoviviparous.

The ratio of the head widths of the nymphal instars to one another are remarkably constant, as in *F. auricularia* according to Henson (1947) and in *A. littorea* according to Giles (1952). In *A. esau* the ratio is about 1·17, in *A. jacobsoni* from Malaya 1·14, but in the specimens from Java collected 19 years earlier it appears to be greater. In view of the comparatively small numbers of the latter species that are available, the figures for it must be considerably less significant ; nevertheless it is apparent that the Javanese specimens of *A. jacobsoni* are considerably smaller in size than those from Malaya.

The antennae of *Arixenia esau* and *A. jacobsoni* are annulate and in both nymphs and adults consist of a long scape freely movable on the antennifer, a short pedicel and a flagellum which increases in length with each moult (fig. 2). As in *Anisolabis littorea* (according to Giles (1952)) and in *Forficula auricularia*, the proximal annulus of the flagellum is long. This annulus is termed " meriston " by Henson (1947), and the name is suitable for denoting the annulus by the division of which the growth of the antenna is brought about ; but, of course, the third segment of the adult antenna cannot properly be so designated. The number of annuli produced by the meriston ranges from three in third instar nymphs to six in the adults (Table I) and does

TABLE I.—*Width of head in mm. and number of annuli in the middle region of the antennae of nymphs and adults of* Arixenia esau *and* A. jacobsoni.

Instar.	Number of annuli.	1·92	2·00	2·08	2·17	2·25	2·33	2·42	2·50	2·58	2·67	2·75	2·83	2·92	3·00	3·08	3·17	3·25	3·33	3·42	3·50	3·58	3·67
A. esau from Malaya, 1952																							
II	0	.	.	4	9	13	25	7	5	1	.	.	.	.	.	.	.	.	.	.	.	.	.
III	3	.	.	.	.	.	.	.	3	4	5	8	5	3	.	.	.	.	.	.	.	.	.
IV	4	.	.	.	.	.	.	.	.	.	.	3	0	3	2	8	5	7	4	2	0	1	.
V	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	0	5	3	2	0
♂	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
♀	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
A. jacobsoni from Malaya, 1952.																							
II	0	.	.	.	1	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
III	3	.	.	.	.	.	.	.	1	0	0	1	.	.	.	.	.	.	.	.	.	.	.
IV	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
V	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
♂	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
♀	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
A. jacobsoni from Java, 1933.																							
III	3	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
IV	4	.	.	.	.	.	.	.	.	.	.	.	1	0	0	0	0	1	1	.	.	.	.
V	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
♂	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	3	3
♀	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE I—*contd.*

Instar.	Number of annuli.	3·75	3·83	3·92	4·00	4·08	4·17	4·25	4·33	4·42	4·50	4·58	4·67	4·75	4·83	Total (N).	Mean width (m).	Standard deviation (σ).	Growth ratio.
A. esau from Malaya, 1952.																			
II	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	64	2·30	·11	
III	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	28	2·72	·12	1·18
IV	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	35	3·14	·30	1·16
V	6	3	1	3	0	2	.	.	.	.	.	.	.	.	.	20	3·65	·23	1·16
♂	6	1	2	3	4	2	2	.	.	.	.	.	.	.	.	15	3·95	·15	1·08
♀	6	.	.	.	.	.	5	4	5	5	4	.	.	.	.	23	4·33	·12	1·19
																185			
A. jacobsoni from Malaya, 1952.																			
II	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	2·28	·	
III	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2·63	·	1·15
IV	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3·33	·	1·13
V	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3·42	·	1·03
♂	6	2	1	1	0	0	1	.	.	.	.	.	.	.	.	5	3·88	·07	1·13
♀	6	.	.	.	.	.	.	.	1	1	0	0	1	1	3	7	4·66	·14	1·36
																19			
A. jacobsoni from Java, 1933.																			
III	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2·00	·	
IV	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3·14	·	1·57
V	5	1	0	2	.	.	.	.	.	.	.	.	.	.	.	3	3·86	·	1·23
♂	6	2	.	.	.	.	.	.	.	.	.	.	.	.	.	13	3·60	0·3	−1·07
♀	6	.	.	1	3	2	2	2	3	1	.	.	.	.	.	14	4·12	·12	1·07
																35			

not appear to vary (cf. *A. littorea*). Nor is there a progressive loss of apical segments, as occurs in *A. littorea* during life (Giles, 1952). In the very few cases in which one antenna of *Arixenia* was damaged or missing, the other was present, so that the number of antennal segments in these animals can be regarded as diagnostic of the instar to which the head width acts merely as a guide.

Description of the Adults of *Arixenia esau* Jordan.

Colour in spirit a deep yellowish-brown similar to that of the nymphs, but somewhat darker on the abdominal tergites. Females considerably larger than males, as in *A. jacobsoni*.

Head.—Prognathous, more or less heart-shaped, broader than long and widest just behind the eyes. Clypeus and frons separated by a curved depression, coronal and frontal sutures not well marked and appearing as pale yellow lines. Muscle attachments pale hairless areas (fig. 1). Eyes small, oval in shape and containing about 50 to 65 facets in the males, 60 to 90 in the females. Antennae inserted laterally, composed of 14 segments. Scape longer than in *A. jacobsoni*, its length being approximately three times its greatest width (fig. 2). Mouthparts similar in both sexes and quite distinct from those of *A. jacobsoni* (fig. 3): they are smaller and less robust; the mandibles are alike and bear three apical teeth, whereas in *A. jacobsoni* the right bears two strong apical teeth and a curved median tooth, whilst the median tooth of the left mandible is divided by a notch. Maxilla smaller and less elongate than in *A. jacobsoni*, while the labium is broad and squat, the galea and lacinia in particular being shortened. Labrum comparatively longer than in *A. jacobsoni*.

Thorax.—The pronotum the longest of the three thoracic tergites and half as long as wide. It is curved posteriorly, whereas in *A. jacobsoni* it is distinctly truncate, not convex, and does not exceed the mesonotum so much in length as in *A. esau*. This is a diagnostic feature in all instars by which the two species may be rapidly distinguished. Sternites wider than in *A. jacobsoni*, truncate and not posteriorly narrowed; legs less densely hairy, as in the nymphal instars. Tarsi with stout claws, wings absent.

Abdomen.—Both sexes have a full complement of tergites as in *A. jacobsoni*; in the male tergites 9 and 10 bear dense tufts of hair which are not found in that species. In the female sternites 2–7 are similar to those of *A. jacobsoni*, but sternite 8 is much reduced and chitinised only along its posterior border. This sternite is represented by a thin membrane in *A. jacobsoni*. Sternite 9 entire and not divided into two separate, heavily chitinised plates as in *A. jacobsoni*, where it is tentatively designated " sternite 8 " by Burr and Jordan (1912). The conspicuous clutch present in *A. jacobsoni* females is lacking in *A. esau*, where the pygidium is rounded and not pointed (fig. 4). Cerci non-segmented, very stout and bent almost at right angles in the male; absolutely distinct from those of male *A. jacobsoni*. In the females the callipers are remote, tapering and almost straight, but shorter and more slender than those of *A. jacobsoni*. The delicate ends appear to be broken in a number of the specimens. The male genitalia are extruded in most of the specimens of *A. esau* (fig. 4*b*, *c*), but this has not occurred in any of the *A. jacobsoni* that I have examined.

Discussion.

The material described above presents a number of problems. It is curious that there were no first instar nymphs since some small bugs (*Loxaspis seminitens* Horvath) (*det.* Dr. W. E. China) were present, suggesting that the collecting had been efficient. Indeed, no first instar nymphs of either species appear ever to have been found. It is possible, of course, that there are in fact only four and not five nymphal instars as I have supposed, but the large size and heavy chitinisation of the smallest of the specimens is such that, even though the animals are probably ovoviviparous, it would appear more likely that some other explanation must be found. Perhaps the first instar nymphs are free-

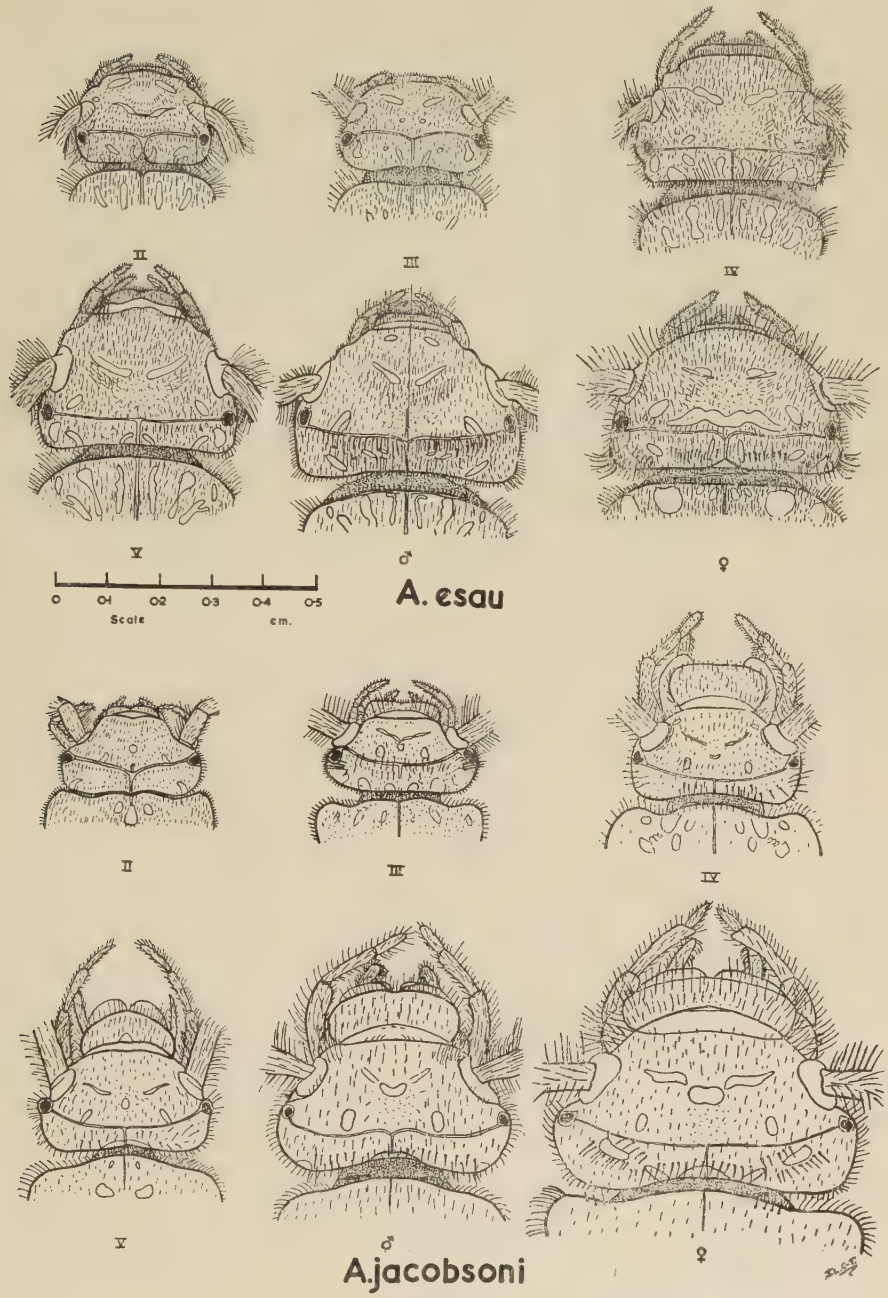


FIG. 1.—Heads of the instars of *Arixenia esau* and *A. jacobsoni* arranged in order and showing progressive change in shape.

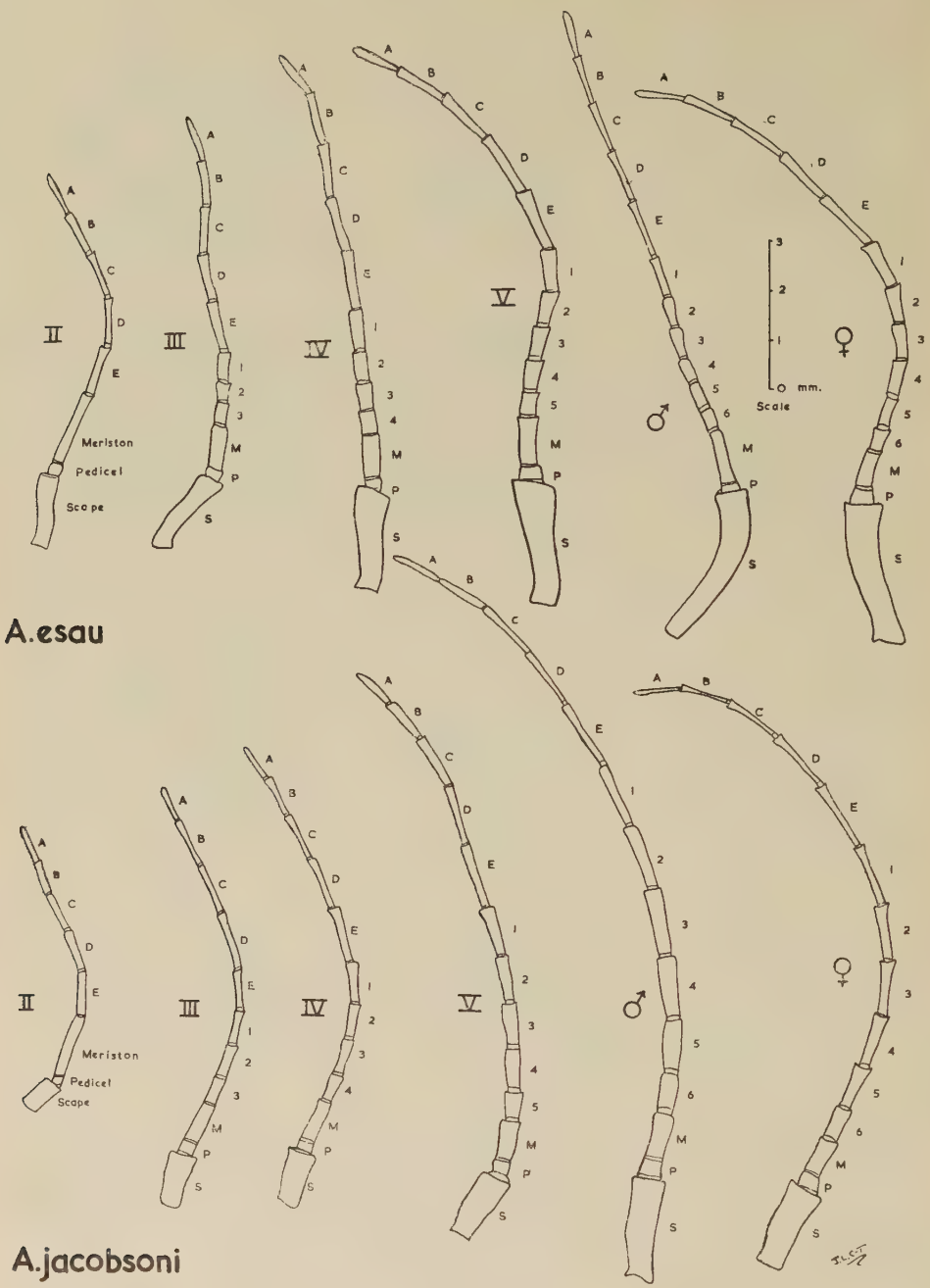


FIG. 2.—Antennae of the instars of *Arixenia esau* and *A. jacobsoni* arranged in order. *S*, scape; *P*, pedicel; *M*, meriston; *1–6*, annuli of the middle region; *A–E*, annuli of the apical region.

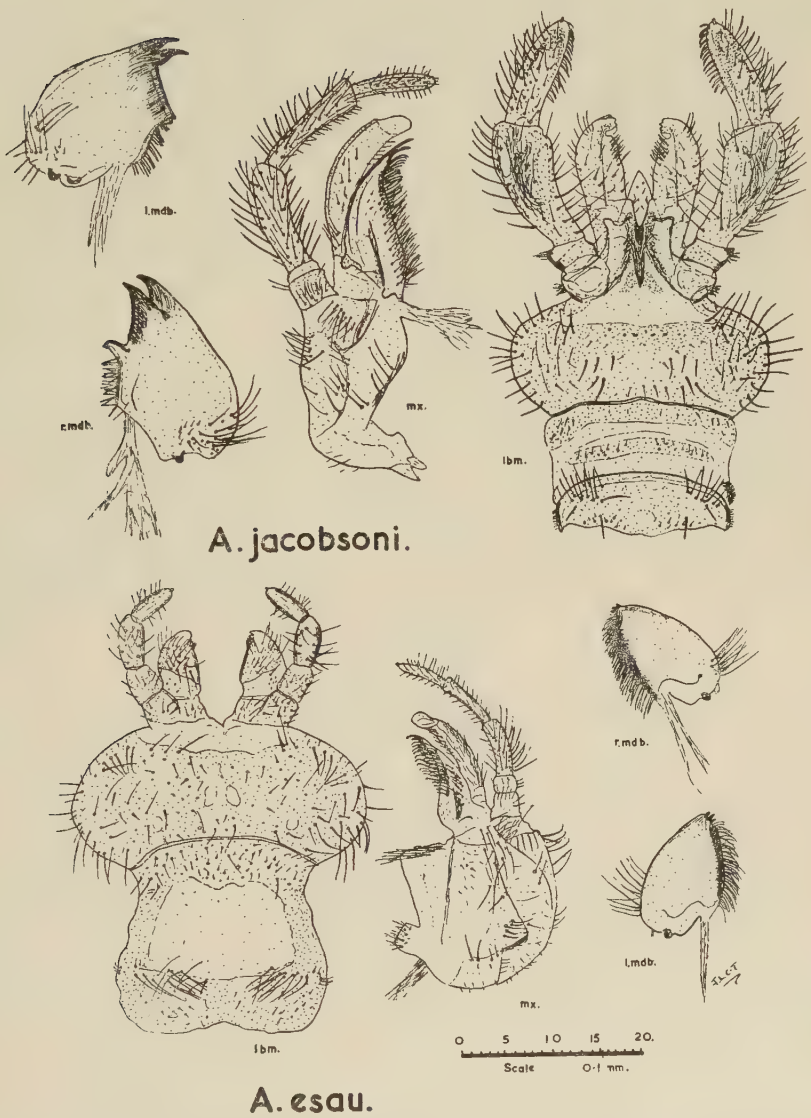


FIG. 3.—Mouthparts of *Arixenia esau* (below) and *A. jacobsoni* (above): *r.mdb*, right mandible; *l.mdb*, left mandible; *mx*, maxilla; *lbm*, labium.

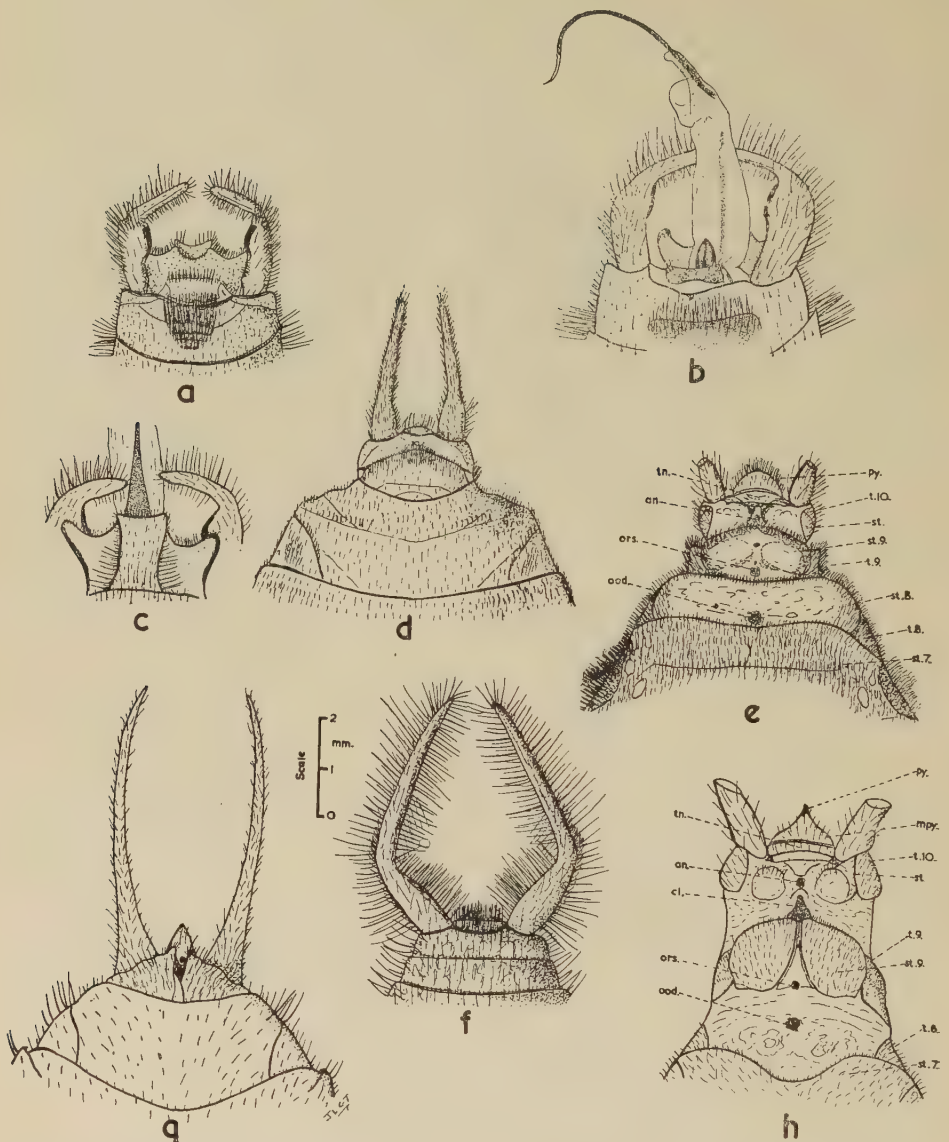


FIG. 4.—Posterior end of abdomen and cerci of *Arixenia esau* and *A. jacobsoni*. *A. esau*: *a*, male, dorsal view; *b*, male with genitalia extruded; *c*, the same seen ventrally; *d*, female, ventral view; *e*, the same stretched out. *A. jacobsoni*: *f*, male, dorsal view; *g*, female, ventral view; *h*, the same stretched out. *st.7–10*, sternites 7–10; *t.8–10*, tergites 8–10; *tn*, telson (= tergite 13); *py*, pygidium; *mpy*, metapygidium; *an*, anus; *cl*, clutch; *ors*, orifice of receptaculum seminorum; *ood*, orifice of oviduct.

living and hide away in crevices. From the growth ratios calculated, it is probable that the mean head widths in first instar nymphs will be found to be about 1·95 mm. in *Arixenia esau* and perhaps slightly more in *A. jacobsoni*.

Again, it is surprising that two related species should appear to occupy the same small ecological niche. Possibly *A. esau* lives mostly on the bodies of bats while *A. jacobsoni* tends to feed more on their guano, to which feeding habit might be related its more robust mouth parts. Unfortunately the preservation of the specimens is such that no recognisable matter can be distinguished in the crop contents of dissected specimens. Against this hypothesis is the fact that *A. jacobsoni* has occasionally been taken from bats and, although the 17 specimens actually found on the bodies of bats by Dr. J. R. Audy were all *A. esau*, this may be due to the fact that *A. jacobsoni* is much less numerous in the present collection (only 19 out of 204 specimens). Alternatively, the bat " colony " may have been an aggregation of bats from various sources. It is not impossible, too, that more than one species of bat was present and that *A. esau* is a parasite of *Cheiromeles torquatus*, while *A. jacobsoni* occurs on *Tardaridus mops*, which is the only host from which I have been able to trace records of the latter species. The proof must await the discovery of further material. Unfortunately no more specimens have been found by Dr. Audy, and the Dusun Wam area has since been heavily infested by terrorists.

A number of small mites taken from the *Arixenia* were returned to Dr. Audy, who suggested that they might represent yet another monotypic family of Sarcoptiformes. They are at present still under investigation.

The bulk of the material on which this study is based has been presented to the British Museum (Natural History) and the Museum of Comparative Zoology, Harvard, Mass., U.S.A.

Summary.

1. An account is given of the discovery in March, 1952 at Dusun Wam, Bukit Lagong Forest Reserve, Selangor, Malaya, of 185 specimens of *Arixenia esau*, previously known only from four nymphs, and 19 specimens of *A. jacobsoni* in a hollow tree inhabited by bats.

2. Both species are probably ovoviviparous and pass through six instars during development, five nymphal and the adult.

3. The mean head widths of successive instars show a growth ratio that is nearly constant for each species. For the majority of specimens the head width provides a means of separating instars, but where overlapping of successive stadia occurs recourse must be made to the antennae.

4. Growth of the antennae takes place by means of division of the meriston (the first segment of the flagellum). In second instar nymphs this is entire, in the third instars it has 3 annuli, in the fourth instars 4, in the fifth instars 5 annuli and in the adults 6.

5. Specimens of *A. jacobsoni* from Java are considerably smaller than examples of the same species from Malaya.

6. Descriptions are given of the adults of *A. esau* and the genitalia and mouthparts of both species are figured.

7. The possible significance of the absence of first instar nymphs and the fact that two related species appear to share the same small ecological niche are discussed.

References.

Burr, M., 1912, A new species of *Arixenia* (Dermaptera). *Ent. mon. Mag.* **48** : 105–106.

——, and Jordan, K., 1913, On *Arixenia* Burr, a suborder of Dermaptera. *Trans. II Int. Congr. Ent.* (Oxford, 1912) **2** : 398–421.

Chopard, L., 1949, Ordre des Dermaptères Leach, 1817, *in* Grassé, P.–P. *Traité de Zoologie* **9** : 745–770.

Giles, E. T., 1952, The growth of the head capsule and antennae of *Anisolabis littorea* (White) (Dermaptera : Labiduridae). *Proc. R. ent. Soc. Lond.* (A) **27** : 91–98.

Henson, H., 1947, The growth and form of the head and antennae in the earwig (*Forficula auricularia* Linn.). *Proc. Leeds phil. Soc.* **5** : 21–32.

Jordan, K. 1909, Description of a new kind of apterous earwig, apparently parasitic on a bat. *Novit. Zool.* **16** : 313–326.

PRELIMINARY OBSERVATIONS ON WEATHER CONDITIONS AND THE ACTIVITY OF BITING FLIES.

By D. S. Kettle.

(*Midge Control Unit, Zoology Dept., Edinburgh.*)

Methods.

There are several references in the literature to the effect of weather conditions on the activity of biting flies in Britain, but none of them is quantitative. This absence of data gives interest to some observations made at Kinlochewe in Wester Ross during a course on Field Entomology in July 1955. The methods adopted here are open to criticism on several counts but, in spite of this, it is considered that the results obtained make a useful contribution to this subject. Over a period of twenty-four hours from 10.30 a.m. on 13th July until the same time on 14th July regular hourly observations were made on weather conditions and on the biting and flying activities of blood-sucking Diptera. Representatives of four genera belonging to three families were caught, the most common being *Culicoides* and *Haematopota*, with occasional *Simulium* and *Tabanus*. In these genera only the females feed on blood and the very few males captured were all *Culicoides*.

The six people participating in this work were arranged in three pairs, each of which was responsible for the observations during the same four-hour shift both day and night. Thus Miss B. A. Hopkins and Mr. R. H. Parish were responsible for the periods 10.30 a.m. to 2.30 p.m. on 13th July and 10.30 p.m. on 13th July to 2.30 a.m. on 14th July. Likewise Miss B. M. Leighton and Dr. R. Varma collected from 2.30 to 6.30 in both the afternoon and early morning and Mr. S. Liu and Dr. D. S. Kettle from 6.30 to 10.30 in the evening and morning.

At the start of each set of observations—at 30 minutes past the hour—one individual made the meteorological observations while the other sampled the air-borne population with a sweep net. Sweeping was done in a straight line between two fixed markers about seventy yards apart and situated at least fifty yards from the base tent. By siting the sweep path this distance from human beings it was hoped to obtain sweep net collections unaffected by the attractiveness of man as a source of food. This goal seems to have been reached since the sweep net and biting collections are not particularly related. The number of sweeps entered in Table I varied between 60 and 72, with a mean of 66. Immediately the " beat " had been covered the collector returned to the tent to examine the catch. On one occasion—6.30 a.m., 14th July—it was very likely that female *C. impunctatus* entered the sweep net to bite the collector while he was removing the catch.

The biting rate was determined by both workers collecting all biting flies which alighted on the legs—ankle to knee—of one individual for 30 minutes in every hour, from 15 minutes before until 15 minutes after the hour. A note was made of the numbers of each genus collected in each 15-minute period, but the catches were not kept separate. These observations were made near one end

of the sweep path in order that the two sets of data should refer to similar populations. Once again, as soon as the period of observation was over, the area was vacated for 15 minutes before the next sweep.

All observations made between 30 minutes before the hour and 29 minutes afterwards are recorded in Table I as being made at the hour. Thus the weather observations and sweep net collections given for 11 a.m. were actually made at 10.30 a.m. and the biting rate from 10.45 to 11.15 a.m.

The meteorological observations included temperature, humidity, light intensity, rain, cloud and wind. Temperature and humidity were determined with a whirling hygrometer. The intensity of illumination was measured with a Weston Master II Lightmeter reading the light reflected from a white card held at right angles to the incident light, *i.e.* in the normal plane. Cloud cover was estimated as the amount in tenths of the total sky obscured by cloud. Wind speed was estimated by its effect upon movable objects. A scale of numbers was used which was not quite the same as the Beaufort scale. The numbers given here tend to indicate lower wind speeds than the Beaufort equivalent. It should be remembered that the wind values are spot readings and windier or calmer periods may well occur between readings.

All the observations were made on an area of windswept moorland east of the Torridon Road (B858) South of Kinlochewe, Wester Ross.

Results and Discussion.

The period of observation began in brilliant hot sunny weather under a cloudless sky, but a breeze soon sprang up and during the late afternoon the sky gradually clouded over, although it remained very hot and bright (Table I, Figs. 1–3). Later during the evening it became cooler and after midnight the cloud cover became complete, the wind increased and it began to rain. This rather cold, dull and windy wet weather continued until almost the end of the observation, when there was a brief period of calm and a break appeared in the clouds. The contrast between the start and end of the period can be seen by comparing the first and last lines of Table I, which gives the 10.30 a.m. weather figures for 13th and 14th July. The 14th is 13·5° F. cooler, its saturation deficiency is 6·5 mbs. less and the illumination is only one eighth that of the previous day.

Haematopota (Table I, Fig. 4).—Two species of clegs were captured, *H. pluvialis* and *H. crassicornis*. Their daily biting cycles are statistically inseparable ($P = 0{\cdot}5$), and in the following account the results will be amalgamated. They were actively attempting to feed during the hot bright morning and afternoon of 13th July. Earlier they had been very troublesome before the observational period began, and it is of interest that none were captured on the 14th, when it was cold and dull. Clegs remained active until sunset at 9 p.m., when the sun descended behind the hills. The intensity of the cleg-biting fell off slowly from the start of the observations at 11 a.m. until 4 p.m. (31 to 21), then there was a sudden decrease in cleg attack between 5 and 6 p.m. (11 and 5), followed, rather unexpectedly, by renewed cleg activity at 7 and 8 p.m. (17 and 19), after which there was very little cleg biting. This dip in the curve of cleg activity required an explanation. It was associated with a small drop in temperature of 4·5° F. and a sudden decrease in illumination to about

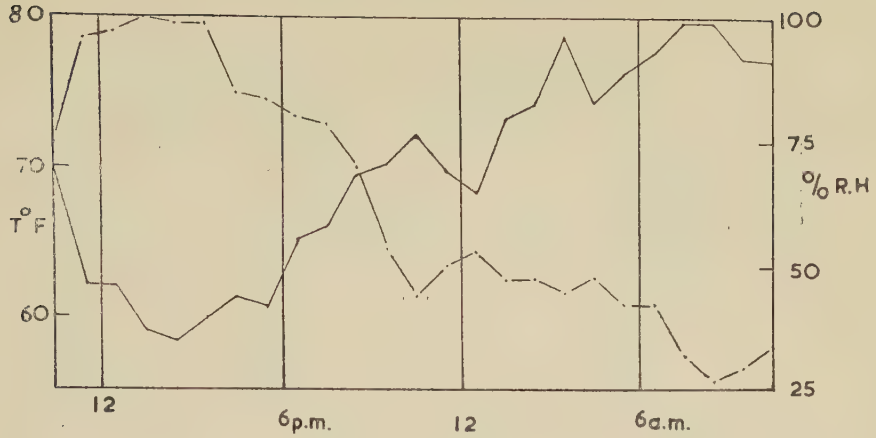


FIG. 1.—Temperature (broken line) and per cent. relative humidity (continuous line) during 24-hour period.

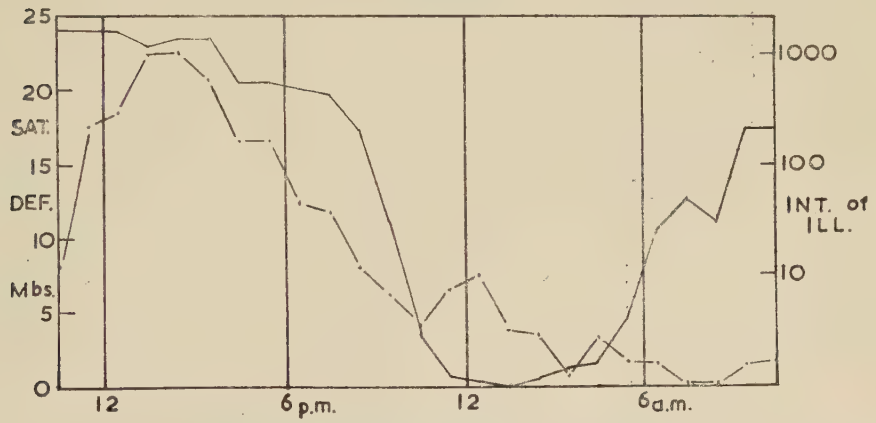


FIG. 2.—Intensity of illumination (continuous line log. scale) in foot candles and saturation deficiency (broken line) during 24-hour period.

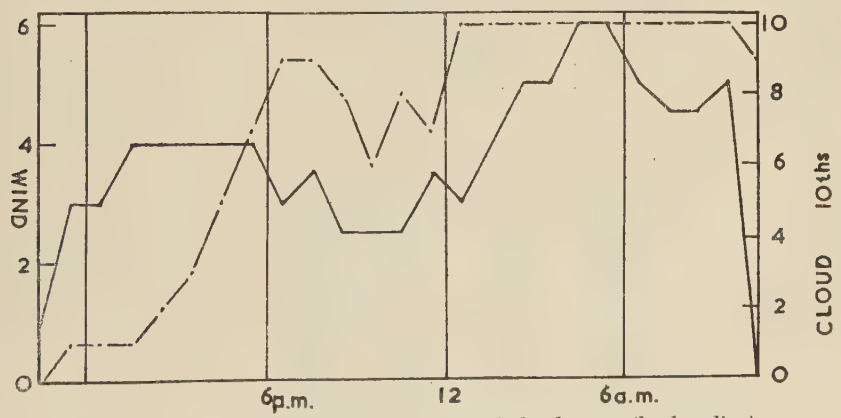


FIG. 3.—Wind speed (continuous line) and cloud cover (broken line) during 24-hour period.

TABLE I.—*Weather conditions and insect catches both in a sweep net and biting.*

Date.	Hour B.S.T.	Dry bulb °F.	Wet bulb °F.	Per cent. R.H.	Sat. def. mbs.	Int. of Ill. f.c.	Rain.	Cloud.	Wind.	No. of sweeps.	Caught in net.				Caught biting.			
											H. pluvialis, females.	*C. impunctatus.* Males.	*C. impunctatus.* Females.	Others.	*C. impunctatus*, females.	*Hæmatopota.* Female *pluvialis.*	*Hæmatopota.* Female *crassicornis.*	Others.
Jul. 13	11 am.	71·5	65·0	69	8·1	1600	Nil	Nil	1	65	1	2	1	1♂ *C. grisescens*	.	23	8	4♀ *Tabanus montanus*
	Noon	78·5	65·5	47	17·5	1600	,,	1/10	3	63	1	.	.	.	.	21	7	.
	1 pm.	79·0	65·5	46	18·4	1600	,,	1/10	3	63	2	.	2	.	.	20	8	2♀ *T. montanus*
	2 pm.	80·0	63·5	37	22·3	1200	,,	1/10	4	65	2	.	1	.	.	16	11	.
	3 pm.	79·5	62·5	35	22·5	1400	,,	2/10	4	68	3	.	.	.	.	18	6	.
	4 pm.	79·5	64·0	40	20·8	1400	,,	3/10	4	71	6	.	.	.	.	18	3	.
	5 pm.	75·0	61·8	44	16·7	550	,,	5/10	4	69	3	.	.	.	.	8	3	.
	6 pm.	74·5	61·0	42	16·7	550	,,	7/10	4	69	3	.	.	.	.	3	2	.
	7 pm.	73·5	63·5	56	12·5	500	,,	9/10	3	70	2	.	1	1♀ *H. crassicornis*	.	15	2	1♀ *Simulium tuberosum*
	8 pm.	73·0	63·5	58	11·9	450	,,	9/10	3–4	65	8	.	.	.	71	14	5	1♀ *S. tuberosum*
	9 pm.	70·0	63·5	69	8·0	200	,,	8/10	2–3	65	12	.	1	.	378	5	.	1♀ *S. reptans* group
	10 pm.	64·5	59·0	71	6·1	30	,,	6/10	2–3	65	9	1	5	2♀ *Simulium latipes*	273	1	.	.
	11 pm.	61·5	57·5	77	4·2	2·5	,,	8/10	2–3	64	.	.	.	.	.	.	.	.
	Midn.	63·5	57·5	68	6·5	0·3	,,	7/10	3–4	63	.	.	.	.	33	.	.	.

TABLE I—*contd.*

Jul. 14	1 am.	65·3	58·5	64	7·5	0·1	,,	10/10	3	72	.	1	4	1♀ *C. fasci-pennis*	5	.	.	.
	2 am.	62·6	59·0	80	3·9	0·0	light	10/10	4	72	.	.	1	1♀ *C. obso-letus*	.	.	.	.
	3 am.	62·6	59·5	83	3·4	0·1	,,	10/10	5	60	.	.	1	1♂ *C. fasci-pennis*	2	.	.	.
	4 am.	61·7	61·0	96	0·7	0·4	,,	10/10	5	68	.	3	.	.	.	.	.	.
	5 am.	62·7	59·5	83	3·3	0·7	,,	10/10	6	69	.	.	1	.	.	.	.	.
	6 am.	60·8	59·0	89	1·9	3·2	Heavy	10/10	6	60	.	.	.	.	19	.	.	.
	7 am.	60·8	59·5	93	1·4	25	Light	10/10	5	63	.	.	22*	.	.	.	.	.
	8 am.	57·2	57·0	99	0·0	45	,,	10/10	4–5	66	.	1	9	.	.	.	.	.
	9 am.	55·4	55·2	99	0·0	30	,,	10/10	4–5	64	.	.	.	.	1	.	.	.
	10 am.	56·3	55·0	92	1·3	200	Nil	10/10	5	66	.	.	.	.	30	.	.	.
	11 am.	58·0	56·5	91	1·6	200	,,	9/10	0									

* Probably includes midges attracted into the net by the presence of the collector.

one-third its previous intensity (1400 to 550 foot candles). This new value was held more or less constant for the next three to four hours. At the start of this period the clegs were relatively inactive but had resumed full activity by the end of this period. Had there been adaptation to the new light intensity?

Two points emerge from the sweep net collections of clegs. Firstly, they gave low catches at a time when clegs were actively biting and high catches when the biting activity was almost over. The highest net catch was made at

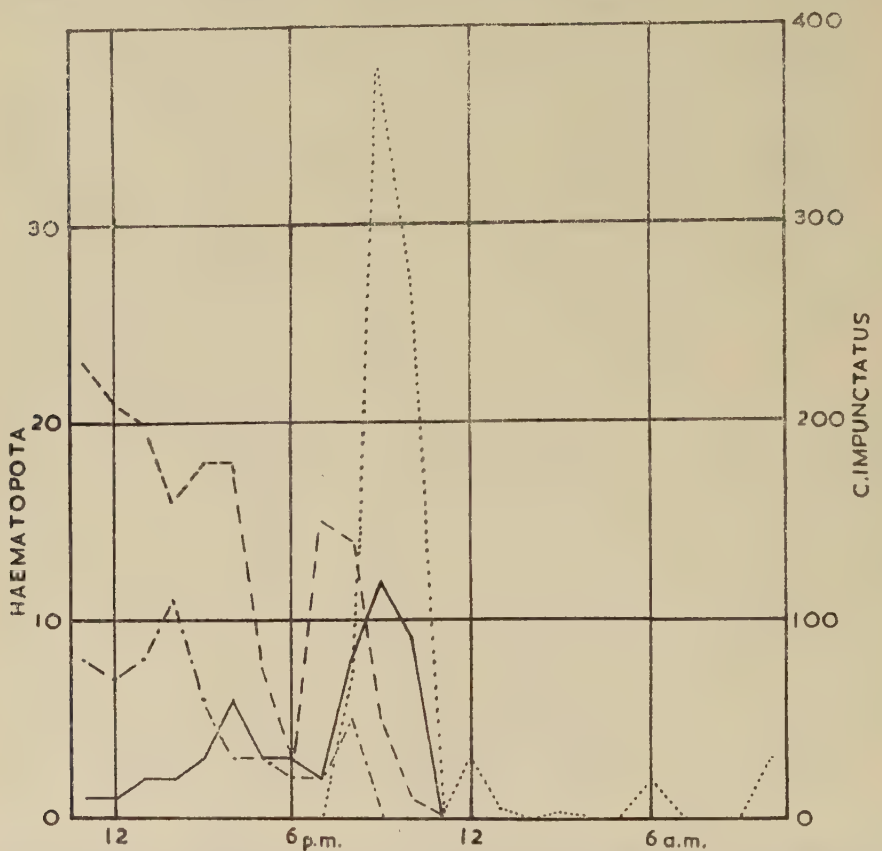


Fig. 4.—Sweep net (continuous line) and biting collections (broken line) of *Haematopota pluvialis* with biting collections of *H. crassicornis* (dash-dot line) and *Culicoides impunctatus* (dotted line) during 24-hour period.

9 p.m. and over half (29 out of 52) of the total sweep net catch was made in the three catches of 8, 9 and 10 p.m. This may indicate either that clegs are not active during the heat of the day unless a suitable host is available or, perhaps more likely, that under warm conditions they are able to avoid the net. Whatever the explanation, it is clear that clegs may be actively flying in the evening when the biting rate is low.

The second point is that, although there were only approximately three times as many *H. pluvialis* as *H. crassicornis* biting (162 : 55), the sweep net collections

were almost pure *H. pluvialis* (52 : 1). This difference is highly significant ($P < 0{\cdot}001$) and probably represents a difference in specific behaviour.

A comparison was made between the numbers of clegs caught biting in the initial and succeeding 15 minute period to find if there were any delay in their finding the host. Although a few more (+ 16 per cent.) clegs were caught during the second period, the difference was statistically insignificant (Table II).

Culicoides (Table 1, Fig. 4). Only one species of *Culicoides* was obtained in any number—*C. impunctatus*. No midges were taken biting until 8 p.m., when the light began to fade rapidly (450–200 f.c.). At this time the temperature was still high (73·0° F.) and the relative humidity moderately low, about 60 per cent. The peak biting activity was attained in the next period, when 378 midges were caught. During this spell the sun descended behind the hill. This produced an immediate outburst in midge activity, as indicated by the capture of 30 adults between 8·45 and 9·00 and 348, or more than eleven times as many, between 9·00 and 9·15. During the subsequent period, in which a similar number of midges were captured (273 cf. 378), the increase between the first and second 15 minute periods was × 1·7 cf. × 11·6.

Little midge activity was encountered during the night when the wind remained high (fig. 3). In the morning, after three consecutive 30 minute periods of exposure for biting (7, 8, 9 a.m.) in which only one midge had been captured, the fourth period (10 a.m.) yielded nothing for 25 minutes, then there was a sudden burst of midge activity and 30 females were captured in a few minutes. This persistent biting continued after the allotted period (10.15 a.m.). It was then noticed that a dead calm prevailed. It is interesting to compare this period with the same time the previous day when preparations were being undertaken. Then it was hot and bright and the clegs were troublesome; now it was dull, calm and humid and the midges were unbearable.

Unlike *Haematopota*, more *C. impunctatus* were captured in the second than in the first 15 minute period of biting (Table II). Even when the sunset figures are omitted the difference is still highly significant. It seems reasonable that there should be a time lag between the arrival of a suitable host in an area, its perception by the insect and the arrival of the insect on the host. The response of a large insect like a cleg is likely to be quicker than that of a tiny midge.

TABLE II.—*Catches of flies attempting to bite in two consecutive* 15 *minute periods; (a) including (b) excluding sunset* 9 *p.m. figures.*

	H. pluvialis *H. crassicornis.* ♀.	*C. impunctatus* ♀. (*a*)	*C. impunctatus* ♀. (*b*)
1st 15 mins. . .	107	196	166
2nd 15 ,, . .	124	696	348
Total . .	231	892	514
P . . .	insig.	<0·001	<0·001

Sweep net catches of *Culicoides* were not particularly interesting, occasional specimens, both male and female, being captured intermittently throughout the 24 hours. Once again there was a lack of correlation between biting and flight activity.

Tabanus.—Six female *T. montanus* were captured attempting to bite around noon under bright sunny conditions.

Simulium.—Two female *S. tuberosum* were taken biting at 7 and 8 p.m. respectively, and a female belonging to the *S. reptans* group at 9 p.m. In the next hour two female *S. latipes* were caught in the net.

Summary.

This paper presents the results of a 24 hour study of weather conditions and the biting and flying activities of *Haematopota pluvialis*, *H. crassicornis* and *Culicoides impunctatus* on open moorland at Kinlochewe in Wester Ross. The importance of high light intensity and warmth in relation to the activity of *Haematopota* sp. and of low light intensity and calm conditions to the activity of *C. impunctatus* is indicated. The results are discussed in some detail.

Acknowledgments.

I wish to record my thanks to the Secretary of State for Scotland for financial assistance in this work, to Miss B. A. Hopkins, Miss B. M. Leighton, Dr. R. Varma, Mr. Liu and Mr. R. H. Parish for participating in the field work ; to Mr. H. Oldroyd and Mr. P. Freeman for assistance with the identification of the Tabanidae and Simulidae respectively, and to the Nature Conservancy, Edinburgh, for accommodation in the Beinn Eighe Field Station.

SPIRACULAR CONTROL OF WATER LOSS IN THE TSETSE FLY.

By E. Bursell.

(Central Tsetse Research Laboratories, East African Trypanosomiasis Research Organisation, Shinyanga, Tanganyika.)

Introduction.

The structure and function of the spiracles of tsetse flies have been the subject of a recent investigation by Geigy and Huber (1952). These workers studied the problem from the point of view of comparative anatomy, and by direct observation of spiracular function under different conditions. They concluded that spiracular regulation was influenced only slightly, if at all, by humidity and failed to find any anatomical evidence for differences in regulatory power between different species.

In view of the wide range of habitats occupied by different species of the genus, and the arid conditions which can be tolerated by several, these findings are rather surprising. The subject was thought to merit reinvestigation by different methods, and it was hoped that direct measurement of rates of water loss would give a more reliable indication of regulatory powers.

Material and Methods.

Flies were exposed to different humidities in cylinders made of perforated zinc sheeting, about 15 cm. long and 1·5 cm. in diameter. Preliminary experiments had shown that the rate of loss per fly was unaffected by the number of flies in the cylinders provided it did not exceed twenty ; in practice ten flies were used in all experiments. Humidities were controlled with potassium hydroxide solution and calcium chloride, except in experiments involving carbon dioxide, when sulphuric acid mixtures were used.

Changes in the weight were determined by transferring the flies to weighed test tubes and re-weighing on an analytical balance which could be read to the nearest tenth of a milligram.

Flies were normally maintained at 80 per cent. Relative Humidity before they were used for experiments ; when they were transferred to dry air the rate of water loss was found to decrease slightly in the course of the first half hour, but after that a steady level of transpiration was maintained. The relatively high initial rates of transpiration may represent the release of small amounts of water from cuticular structures originally in equilibrium with the air at 80 per cent. R.H. ; if so, they are not strictly relevant to the present study, and values given below will refer to the steady rates of loss.

At low humidities the weight loss was such that a reliable estimate of transpiration rate could be obtained in an hour ; at higher humidities the duration of exposure had to be prolonged (up to 3–4 hours in 98 per cent. R.H.) in order that a reasonable change of weight should be recorded.

To determine rates of loss in carbon dioxide/air mixtures special desiccators were used ; these were provided with small holes through which the perforated

cylinders could be introduced without appreciably changing the composition of the air inside. Before and after introduction of the cylinders the holes were covered with glass slides sealed with vaseline.

All experiments were carried out in the dark ; it has been found that under these conditions any differences in the rate of water loss at various humidities cannot be ascribed to differences in activity (Bursell, 1957), so that any effect of humidity on rate of water loss is not simply due to differences in activity. Some idea of the general level of activity was gained by suspending tubes of similar dimensions to the perforated zinc cylinders, but made of bolting silk, on a very thin glass rod. The movements of the end of the rod were recorded on a smoked drum. These records show that under the conditions of the experiments flies are almost continually active, so that the rates of water loss recorded represent transpiration during sustained activity.

Unfed flies of *Glossina morsitans* Westw. were used for all the experiments to be described.[1] In such flies excretion of water and waste products occurs soon after emergence from the pupa ; once they have been desiccated for some time the amount of weight lost in this way is negligible.

For the sake of convenience, rates of water loss have been estimated from recorded changes in weight, and loss of solid materials has been ignored. In the course of starvation appreciable amounts of fat are used, but since 1·07 mg. of water is produced for every mg. of fat oxidised (Wigglesworth, 1953), the consumption of fat does not involve any loss in weight. The loss of solids other than fat is negligible except for flies in the last stages of starvation, and such flies have not been used.

Weight loss is expressed as mg. per fly per hour ; all the experiments (except one, see Table III) were carried out between February and May, and during this time of the year the size of flies shows little seasonal variation (Jackson, 1953). In batches of ten flies, such as have been used throughout, differences in mean size are small, and in view of the large amount of uncontrolled variation it has been thought unnecessary to correct for them. The average weight of a *G. morsitans* at emergence from the pupa is about 25 mg., so that to obtain the percentage weight loss values must be multiplied by four.

Results.

1. Water loss in the absence of spiracular regulation.

In the tsetse fly, as in most other insects, the spiracles can be made to open by exposing the fly to carbon dioxide. Care must be taken, however, that the tension of carbon dioxide is sufficiently high to cause complete and sustained opening. The threshold for day-old flies is about 10 per cent. carbon dioxide ; below this value there is a rapid decrease in the rate of water loss during exposure to the carbon dioxide/air mixture, the rate of decrease being greater the lower the carbon dioxide tension (see Table I) ; with 5 per cent. carbon dioxide the rate of water loss returns to the level characteristic of normal air in one and a half hours, while in 8 per cent. it takes about twice as long. In 10 per cent. carbon dioxide the rate of water loss is maintained at a constant level, and this level is the same for all concentrations of carbon dioxide above

[1] The pupae from which the flies emerged had been collected in Singida, Central Province, and would be referred to the subspecies *morsitans* Vanderplank.

the threshold. It represents the rate of water loss in the absence of spiracular regulation.

TABLE I.—*The water loss of* G. morsitans *during exposure in dry air and in different concentrations of carbon dioxide.*

	Rate of loss (mg./fly/hr.)		
I. In air	0·30	0·25	0·28
II. In CO_2	(5%	8%	10%)
Time (min.)			
15	0·69	0·86	1·00
45	0·46	0·75	1·00
75	0·31	0·60	1·02
115	0·30	0·51	1·00

Three groups of ten flies were tested, first in air for one hour and then in the carbon dioxide/air mixtures.

The carbon dioxide threshold for sustained opening of the spiracles is influenced by the physiological state of the fly. Thus in newly-emerged flies 8 per cent. carbon dioxide is sufficient to cause the spiracles to remain open; in day-old flies the threshold is about 10 per cent., while in four-day-old flies which have been kept in 80 per cent. R.H. since emergence the carbon dioxide concentration has to be increased to 20 per cent. to prevent closure. These changes in sensitivity to carbon dioxide may be of some biological significance, and it is hoped to investigate the problem further in connection with studies on respiration.

The rate of water loss in dry air of flies whose spiracles have been opened by exposure to carbon dioxide is about 1·10 mg. per insect per hour. If all the spiracles are blocked with paraffin wax the rate of loss, representing transpiration from the general body surface, is about 0·09 mg. per insect per hour. Active regulation of water loss by the spiracular complex will be capable of affecting the rate of water loss within these limits.

2. The effect of water content on spiracular regulation.

Preliminary experiments showed that the rate of water loss decreased in the course of desiccation, the rate of decrease being most rapid in the early stages. Since neither the water loss in carbon dioxide/air mixtures nor the water loss after blocking of the spiracles show any change with time, this decrease must be caused by changes in the degree of spiracular control.

To investigate the phenomenon in greater detail flies were exposed to 80 per cent. R.H. for different lengths of time, after which their rate of water loss was determined in dry air. The results are shown in Table II. It is clear that the longer the duration of exposure the lower is the rate of transpiration; but the data do not permit a decision as to which of three variables are causally related to rate of loss, whether age as such, or fat content, or water content. To decide between these possibilities two further experiments were carried out. In one, flies were desiccated rapidly by exposure to 0 per cent. R.H.; in the other, water content was maintained at high levels but the fat content reduced

by keeping the flies for two days in saturated air. In these experiments the oldest flies with the lowest fat content showed the highest rate of water loss, which is the reverse of the relation obtained in the previous group of experiments; clearly neither age nor fat content can be significant in relation to spiracular regulation. But if the data are compared on the basis of water content there is good agreement, the rate of water loss being lower the lower the water content in both sets of experiments.

TABLE II.—*The effect of desiccation on the rate of water loss in dry air.*

Initial desiccation in	Age (hours).	Mean fat content % dry weight.	Mean water content % fatless wet weight.	Mean rate of water loss (mg./fly/hr.) at 0% R.H.	N.
80% R.H.	1	25·3	72·8	0·365	4
,,	18	20·9	71·8	0·286	7
,,	42	15·6	67·8	0·250	2
,,	66	11·2	66·4	0·190	5
,,	90	9·3	65·0	0·170	2
0% R.H.	24	17·5	70·2	0·263	3
100% R.H.	48	12·2	72·0	0·305	3

Fat content is expressed as a percentage of the total dry weight; water content as a percentage of the fatless wet weight.

N is the number of experiments in each of which ten flies were used.

In figure 1 the data for all experiments have been plotted on a single graph; in spite of great variability the data show a strong positive correlation between water content and rate of water loss. It may be concluded that depletion of water reserves causes a decrease in transpiration, and that this change is brought about by spiracular control.[2]

3. The effect of humidity on spiracular regulation.

Figure 2*a* shows the rate of loss of water of flies in air and in 15 per cent. carbon dioxide at different relative humidities. The relation between humidity and transpiration when the spiracles are kept open with carbon dioxide is approximately rectilinear, and so it is when the spiracles are blocked with paraffin wax. But with normal flies tested in air the curves are asymptotic, tending to flatten out at lower humidities. It is apparent that this departure from the rectilinear must be caused by spiracular regulation, the degree of closure being greater the lower the humidity. By comparing, at any particular relative humidity, the water loss of normal flies with the upper and lower limits of loss, represented by the carbon dioxide-line and the spiracle-blocked-line, it is possible to get an idea of the extent of spiracular closure at that humidity. For one-day-old tenerals the degree of closure increases from about 20 per cent. at 90 per cent. R.H. to 75 per cent. in dry air; for three-

[2] It must be emphasised that this decrease in transpiration is not a simple consequence of a decrease in rate of respiration; no difference in the level of activity can be demonstrated with the, admittedly rough, kymographic method; and results obtained in the field (Jackson, 1946) and in the laboratory (Bursell, 1957) show that, if anything, there would be an increase in activity with age.

day-old flies it increases from about 50 per cent. at 90 per cent. R.H. to 85 per cent. in dry air (see fig. 2*b*).

These results show that the degree of spiracular regulation is influenced on the one hand by the humidity of the ambient atmosphere, on the other by the physiological state of the insect in such a way that the more precarious the state of its water reserves the more stringent is the regulation.

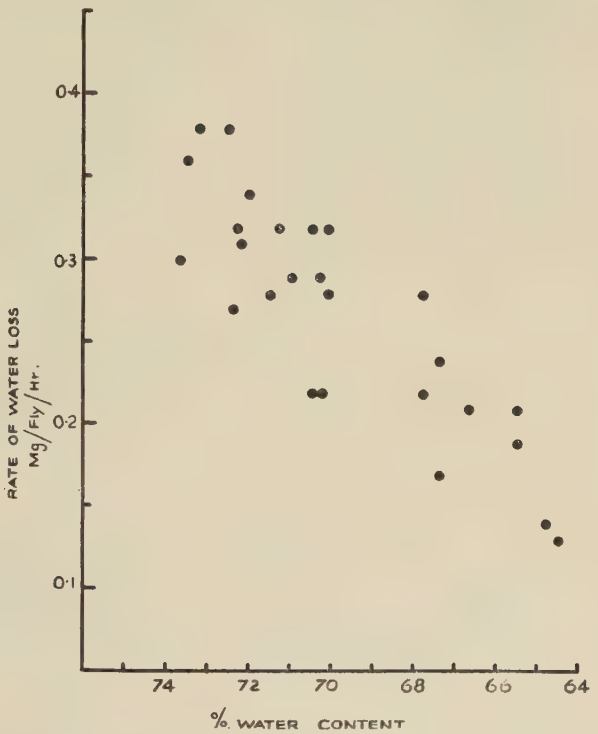


FIG. 1.—The correlation between water content and rate of water loss in *G. morsitans*. $r = 0{\cdot}8390$; $P < 0{\cdot}001$.

Water contents were determined at the end of experiments which included exposure to carbon dioxide, so that water contents at the time when the rates of loss in air were measured would be about 1·5 per cent. higher than quoted.

It seemed possible that this complex integration might be brought about by some one of the various sensory structures which beset the external surface of the tsetse fly, and attempts were made to identify the sense organs responsible. The most likely possibilities were the antennal sense organs (Jobling, 1933), the tarsal sense organs (Lewis, 1954), the sense organs on the leading edges of the wings (C. T. Lewis, *personal communication*), the spiracular filters (Geigy and Huber, 1952), the palps (Jobling, 1933) and the abdominal hair plate.[3] The procedure was to cut off the appendages bearing these organs (wings,

[3] This structure, which represents the first abdominal sternite, does not appear to have been previously described; it is situated on the anteroventral surface of the abdomen and consists of a plate bearing numerous long sensory hairs.

tarsi, palps), to extirpate the sense organs themselves (spiracular filters) or to render them functionless by covering them with paraffin wax (antennae, abdominal hair plate), and then to determine the rates of water loss in a series

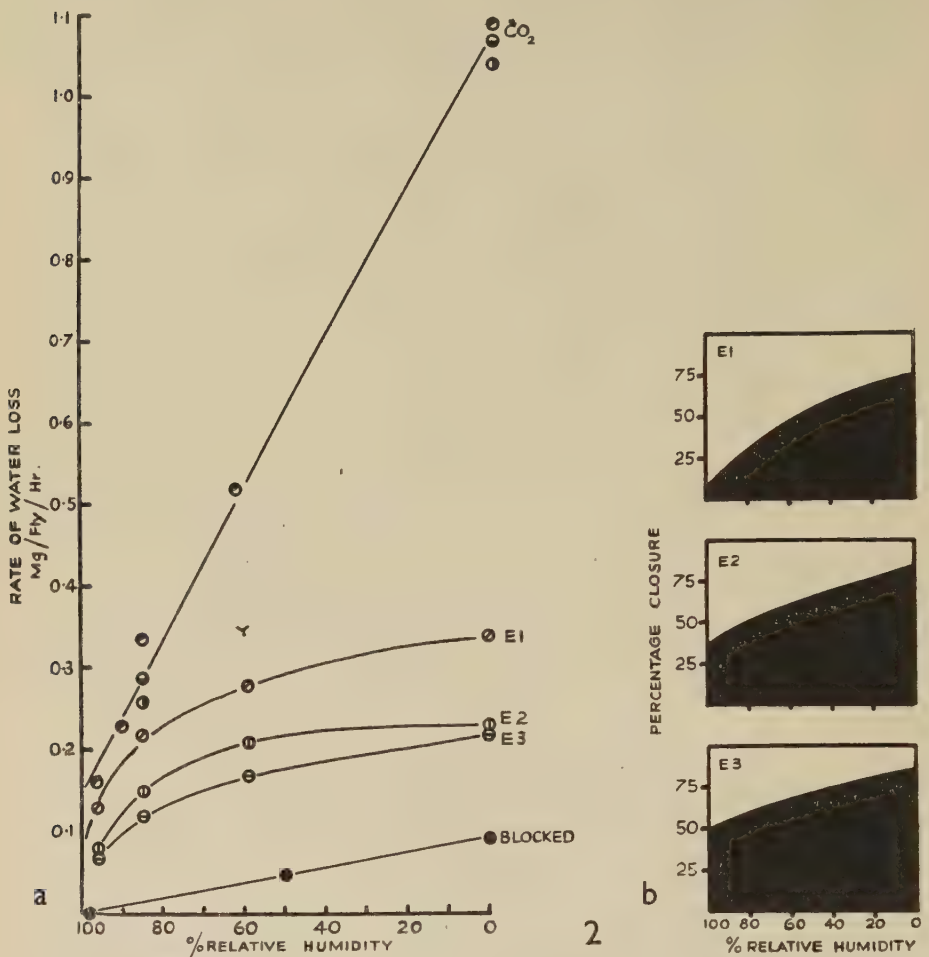


Fig. 2.—(*a*) The water loss of *G. morsitans* at different relative humidities. *Open circles*, flies in air ; *Half-closed circles*, flies in carbon dioxide ; *Closed circles*, flies with blocked spiracles.

◑ ◐, one day after emergence ; ◑ ◑, two days after emergence ; ⊖ ◒, three days after emergence.

(*b*) The effect of humidity on the degree of spiracular closure one, two and three days after emergence.

of relative humidities as compared with concurrently run control groups. For the sake of simplicity only the results in 0 per cent. R.H. have been included in Table III ; they show that whatever the treatment the degree of spiracular regulation is about the same for control and experimental groups, and this is

borne out by results at higher humidities. It may be concluded that none of these receptors is concerned with the mechanism of spiracular control.

TABLE III.—*The effect of eliminating various sense organs on spiracular control of water loss in dry air.*

Age of flies (days).	Receptors.	Rate of water loss (mg./fly/hr.). In air Cont.	In air Exp.	In CO_2 Cont.	In CO_2 Exp.	% closure. Cont.	% closure. Exp.
1	Spiracular filter . . .	0·41	0·34	1·05	0·85	67	67
1	Tarsal sense organs . .	0·34	0·29	1·10	1·07	75	80
2	Antennae	0·21	0·25	0·98	1·01	86	83
2	Wing sense organs . .	0·25	0·26	1·20	1·28	86	86
2	Palps	0·25	0·27	1·12	1·02	84	81
2	Abdominal hair plate . .	0·17	0·17	0·90	0·89	90	90*

Flies were kept in 80 per cent. R.H. after emergence from the pupae, and allowed at least 12 hours to recover from operative shock.

Each group of ten flies was tested first in air and then in carbon dioxide.

* These experiments were done at the end of the dry season when the mean weight of teneral males was only 20 mg., which accounts for the low rates of loss.

DISCUSSION.

It has been shown that, in the teneral tsetse fly, spiracular control of transpiration is markedly influenced by humidity. This effect is contrary to the findings of Geigy and Huber (1952), whose results indicate that the opening and closing of spiracles is little, if at all, affected by humidity. Attempts have been made to repeat the observations of the Swiss workers with teneral flies of *G. morsitans* ; the insects were secured in small clamps and the metathoracic spiracles exposed by removal of the spiracular filters. It was found that under these conditions opening of the spiracles was always a momentary phenomenon associated with struggling. In desiccated flies, however, the spiracles appeared to open less completely during a bout of struggling than in newly-emerged flies, and it is possible that such differences in the degree of opening during activity may be the basis of the regulation of water loss described above.

With newly-fed flies, on the other hand, sustained opening of the spiracles in the absence of muscular activity was observed, suggesting that in such flies there is little spiracular control of water loss. This is in accord with the results of Geigy and Huber (1952), whose flies were given daily opportunity to feed. It seems possible that the failure of the Swiss workers to find evidence of regulatory power may be attributed to their use of recently-fed flies ; in other words that spiracular regulation of water loss occurs only when water reserves have been to some extent depleted.

The relation between humidity and water loss has been studied by a number of workers (Buxton and Lewis, 1934 ; Mellanby, 1936 ; Jack, 1939) using vari-

ous species of tsetse. Particular attention has been paid to the observation that groups of flies which have been starved in widely different humidities show comparatively slight differences in water content (see also Buxton, 1955).

Buxton and Lewis (1934) have coupled this observation with the finding that *Glossina tachinoides* consumes more fat in dry than in wet air, and suggest that this increased fat consumption with consequently increased production of metabolic water in dry air may account for the apparent discrepancy. This view has been challenged by Mellanby (1936) working with *G. palpalis*. The present investigations have shown that the drier the insect, and the drier the air, the greater is the extent of spiracular control. These relations would be expected to give the fly a certain independence of differences in ambient humidity, and so account for the relatively constant water contents. For instance, a teneral fly starved at 80 per cent. R.H. will have its spiracles three-quarters open and will lose water at a fairly high rate in spite of the low saturation deficiency; whilst a fly in 0 per cent. R.H. will keep its spiracles three-quarters closed and so lose relatively little although the saturation deficiency is high. Despite this initial regulation the fly starved at 0 per cent. R.H. will lose rather more water than that starved at 80 per cent. R.H.; but this difference which arises in the course of desiccation will bring in the second aspect of regulation, namely the dependence of spiracular closure on water content. As the fly in 0 per cent. R.H. loses more water than the fly in 80 per cent. R.H. its water content will be lower and its regulation more stringent; indeed the rate of loss in 0 per cent. R.H. comes to be lower than that at 80 per cent. R.H. despite the much higher saturation deficiency. Reference to figure 2*a* shows that the rate of loss of day-old flies in 80 per cent. R.H. is greater than the rate of loss of two-day-old flies in 0 per cent. R.H., which is an illustration of this principle. It is thought that the absence of a strong correlation between the water content of starved flies and the humidity at which they are starved finds adequate explanation in these terms, and that it is unnecessary to postulate differences in the amount of metabolic water produced to account for the effect. An increase in fat consumption does occur in dry air, in consequence of the orthokinetic reaction to humidity; all the species studied have been found to be more active in dry than in wet air (Bursell, 1957). The suggestion (Buxton, 1955: 93), however, that this increase in activity is of direct advantage in relation to water balance demands further substantiation.

Departure from a rectilinear relation between rates of transpiration and humidity have been found in a number of other insects (see, for instance, Wigglesworth, 1953). It has been suggested that the relatively low transpiration values recorded in dry air may be caused by the rate of loss of water from the spiracles exceeding its rate of replenishment through the tracheal walls, so that the permeability of the latter becomes a limiting factor (Mellanby, 1935). If this were so one would expect the phenomenon to find its strongest expression when transpiration is measured in carbon dioxide/air mixtures, since under these conditions the rate of loss through the spiracles is at its highest. In fact it has been shown that under these conditions the relation between humidity and transpiration approaches closely to rectilinearity; so this explanation clearly does not hold good for the tsetse fly, and the departures shown by normal flies must be attributed entirely to spiracular control.

Acknowledgments.

My thanks are due to Mr. Yahya Mohamed for his careful estimation of fat and dry weight of flies; to Professor D. W. Ewer, Dr. K. Mellanby, Dr. J. P. Glasgow, Mr. W. H. Potts, Mr. E. F. Whiteside and Mr. D. L. Johns for helpful discussion of the manuscript; and to the late Dr. C. H. N. Jackson for his constant encouragement and support.

Summary.

1. The rate of water loss of *G. morsitans* decreases in the course of desiccation; this decrease is brought about by a progressive increase in the degree of spiracular control.

2. The rate of water loss of flies whose spiracles have been blocked, or of flies whose spiracles are kept open by exposure to carbon dioxide, is a linear function of humidity. With normal flies, on the other hand, the curve is asymptotic, rates of loss in dry air being relatively low. It is shown that this departure from the rectilinear relation must be caused by spiracular control; in other words, the drier the air the greater the degree of closure of the spiracles.

References.

Bursell, E., 1957, The effect of humidity on the activity of tsetse flies. *J. exp. Biol.* **34**. (*In press*).

Buxton, P. A., 1955, *The Natural History of Tsetse Flies.* (London School of Hygiene and Tropical Medicine. Memoir No. 10.)

——, and Lewis, D. J., 1934, Climate and tsetse flies: Laboratory studies upon *Glossina submorsitans* and *tachinoides*. *Philos. Trans.* (B) **224**: 175–240.

Geigy, R., and Huber, M., 1952, Untersuchungen über Bau und Funktion der Stigmen bei verschiedenen *Glossina*-Arten und bei *Stomoxys calcitrans*. *Acta trop., Basel* **9**: 233–263.

Jack, R. W., 1939, Studies on the physiology and behaviour of *Glossina morsitans* Westw. *Mem. Dep. Agric. S. Rhod.* No. 1.

Jackson, C. H. N., 1946, An artificially isolated generation of tsetse flies (Diptera). *Bull. ent. Res.* **37**: 291–299.

——, 1953, Seasonal variation in the mean size of tsetse flies. *Ibid.* **43**: 703–706.

Jobling, B., 1933, A revision of the structure of the head, mouth parts and salivary glands of *Glossina palpalis* Rob.-Desv. *Parasitology* **24**: 449–490.

Lewis, C. T., 1954, Studies concerning the uptake of contact insecticides. I. The anatomy of the tarsi of certain Diptera of medical importance. *Bull. ent. Res.* **45**: 711–722.

Mellanby, K., 1935, The evaporation of water from insects. *Biol. Rev.* **10**: 317–402.

——, 1936, Experimental work with the tsetse fly, *Glossina palpalis*, in Uganda. *Bull. ent. Res.* **27**: 611–633.

Wigglesworth, V. B., 1953, *The Principles of Insect Physiology.* London.

NOTES ON THE CHORIOTHETE AND MILK GLAND OF *GLOSSINA* AND *HIPPOBOSCA* (DIPTERA).

By E. Bursell and the late C. H. N. Jackson.

(*Central Tsetse Research Laboratories, East African Trypanosomiasis Research Organisation, Shinyanga, Tanganyika.*)

Since the discovery of the choriothete (Jackson, 1948) a number of observations have been made which extend our knowledge of this organ. Some of these findings bear on certain aspects of larval respiration (Bursell, 1955); but, since they could not readily find a place in a paper dealing specifically with this latter problem, it was decided to publish them separately together with some incidental observations on the milk gland.

1. The Cycle of Development of the Choriothete During Pregnancy.

Serial sections of uteri of *Glossina morsitans* Westwood were cut at different times after larviposition. From these reconstructions were made of the choriothete, as shown in figure 1.

Figure 1*a* shows the choriothete attached to the chorion of an embryo two days old. At this stage the choriothete is a massive structure consisting of a sheet of glandular cells, several layers thick, overlying a well-developed cushion of muscle below which is a fairly thick layer of connective tissue. Two substantial muscles run anteroventrally from the choriothete to be inserted on the ventral body wall about a third of a millimetre in front of it.

Two days later (fig. 1*b*) the embryo has hatched but the chorion is not yet detached from the choriothete. The structure of the latter has remained unchanged but there has been a slight backward shift and it has decreased somewhat in size, possibly indicating that degenerative changes commence before the removal of the first instar skin. On the other hand, it may be that these apparent changes can be attributed to individual differences between the flies examined.

After removal of the chorion the choriothete becomes attached to the integument of the first instar. The first moult occurs soon afterwards and the first instar exuvium is removed by the choriothete. During subsequent phases of pregnancy it can be seen lying in a depression of the uterus floor behind the choriothete, in close association with the chorion.

After the first moult the choriothete undergoes rapid degeneration, the first component to be affected being the muscular cushion. By the sixth day this has been reduced to a narrow sheet underlying the anterior part of the glandular epithelium, which has also decreased in extent (fig. 1*c*). The muscles attaching the choriothete to the body-wall have disappeared completely. While these degenerative changes are taking place the whole organ becomes displaced backwards, either by pressure of the developing larva or by active migration, and comes in part to underlie the chorion and first larval instar exuvium.

Three days later this process of backward extension has proceeded still further and the whole choriothete has become reduced to a single layer of glandular cells associated with a very thin sheet of connective tissue (*see* Jackson, 1948, Pl. VIII). No trace is left of the muscular parts of the organ.

By the time the larva is ready to be deposited the choriothete has started to regenerate; when the new egg descends into the uterus it has reached the stage shown in figure 1*a* and the cycle is repeated.

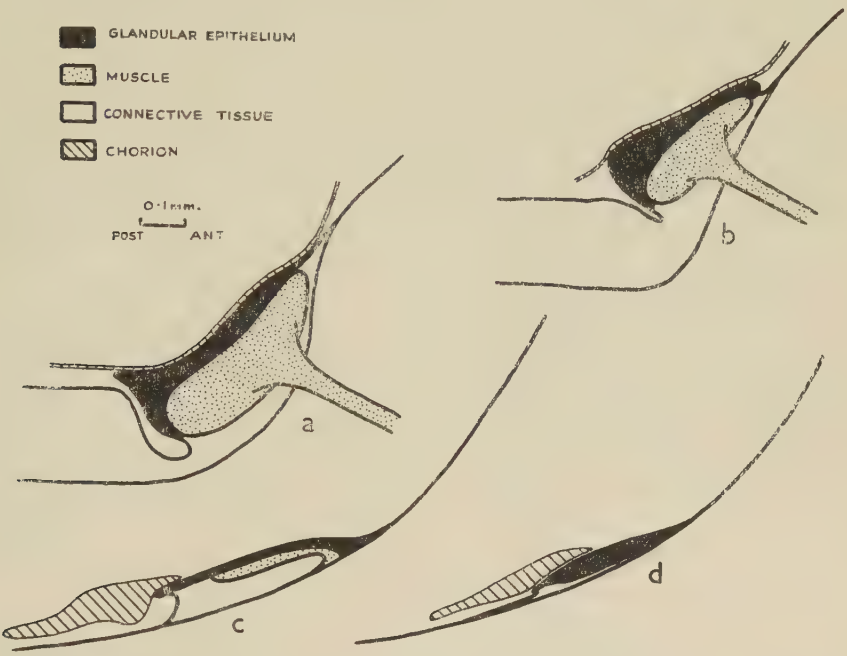


Fig. 1.—Sagittal section of the anterior part of the uterus floor showing regressive changes of the choriothete during pregnancy. (*a*), (*b*), (*c*), (*d*)—2, 4, 6 and 9 days respectively after larviposition. The interlarval period at the time when the serial sections were prepared was about 11 days. Horizontal shifts were determined with reference to the U-bend of spermathecal ducts above the dorsal wall of the uterus.

2. The Fate of the Chorion and of the Larval Exuvia.

In sections of embryos and first instar larvae, the choriothete has invariably been found to adhere intimately to the chorion and first instar integument respectively; and in all the sections examined of uteri containing later instars it has been possible to identify both chorion and first instar exuvium folded together behind the choriothete. There can be little doubt that the choriothete is responsible for the removal of both these membranes.

During a study of the respiratory lobes of the tsetse (Bursell, 1955) it was found that the second instar skin is not shed until just before larviposition; by that time the choriothete is greatly reduced and manifestly incapable of removing the exuvium (*see* fig. 1*d*). This is contrary to the findings

of Jackson (1948), who published a photograph of the chorion with first and second larval skins lying above the reduced choriothete. At that time the presence of spines was accepted as a criterion of a second instar larva (Burtt and Jackson, 1951); but subsequent examination of fresh and sectioned first instar larvae (identified as such by the presence of an egg tooth) showed that the first instar larva also bears a patch of spines dorsally between the respiratory openings, although these spines are very inconspicuous compared with those of the second instar.[1] Subsequently a preparation was obtained in which spines could be identified on the exuvium which was folded with the chorion behind the choriothete, although the larva contained in the uterus had not yet shed its second instar integument. There can be no doubt that the spines figured by Jackson (1948) are spines of the first instar, and that the second instar exuvium is shed without the intervention of the choriothete.

The mechanism of shedding of the second instar exuvium is not clear. After its attenuation by the action of exuvial fluids it probably splits along lines of weakness during growth of the third instar larva; it may then be sloughed off on the spines of the vagina by peristaltic movements during or just prior to parturition.

With regard to the ultimate fate of the chorion and larval skins, it has recently been reported that in *G. palpalis* these membranes are partially dissolved by a fluid secreted by the choriothete, and that undissolved particles may subsequently be extruded (Hoffmann, 1953). In 15 sets of serial sections examined by us the chorion and first instar skin have shown no signs of lysis; in one case they have been found intact in the uterus after deposition of the larva; in two cases they have been recovered unchanged from faecal debris in the maintenance tubes; and in most third instar abortions (which are common at Shinyanga) the folded chorion and first larval exuvium can be identified adhering to the skin of the third instar larva anteroventrally, that is, in the position which they occupied with respect to the larva *in utero*.

The second instar skin, readily identified by the stout spines between its large tracheal trunks, can also be found in association with third instar abortions, but this membrane usually adheres near to the anus of the third instar larva, thus confirming that its removal is independent of the action of the choriothete.

In addition to flies of the *morsitans* group available at Shinyanga, some specimens of *G. palpalis* were obtained from Uganda; in these also the chorion and exuvium of the first instar larva could be found intact in the choriothete pocket up till the end of pregnancy. The balance of evidence is thus in favour of the view put forward by Newstead, Evans and Potts (1924) that "the chorion of the egg together with the two effete larval skins . . . are expelled after the act of parturition".

3. The Mechanism of Choriothete Action.

The posterior cavity in the choriothete, described by Jackson (1948), is not a regular feature of this organ. Of four preparations of the choriothete recently examined at the height of its development it is present in only one.

[1] *G. palpalis* Robineau-Desvoidy differs from flies of the *morsitans* group in that the spines of the first instar larva are almost as well developed as those of the second instar. The larvae examined by us belonged to the subspecies *fuscipes*; Roubaud (1909) and Hoffmann (1953), whose findings are discussed below, worked with other subspecies.

It is thought that this sinus is an artefact caused by shrinkage during fixation, and that the active removal by the choriothete of the chorion and first larval integument is based entirely on muscular activity. Muscle fibres can be seen passing between cells of the glandular epithelium to be inserted near the surface (it has unfortunately not been possible to get a satisfactory photomicrograph of this phenomenon). These muscle fibres are presumably responsible for throwing the membrane into folds over the surface of attachment to the egg shell. Simultaneous contractions of the large choriothete muscles attached to the ventral surface of the parent fly would pull the membrane forwards and downwards, thus freeing the larva by way of the mid-dorsal longitudinal split.

4. The Choriothete of *Hippobosca longipennis* Fabricius.

Specimens of *Hippobosca longipennis* were obtained from the spotted hyaena, *Crocuta crocuta* Erxleben, and serial sections were cut of uteri containing embryos and larvae at different stages of development. Plate I shows that a choriothete is present in this group also, characterised, as in *Glossina*, by extensive muscular development. In this species the process of degeneration during pregnancy is even more striking than in the tsetse ; in the uterus containing a third instar larva the choriothete is barely distinguishable from the adjoining uterine epithelium. Another difference is that in *Hippobosca* it has not been possible to trace the chorion after its removal from the embryo ; it is either voided immediately or is very rapidly dissolved by the choriothete, for it does not persist in the uterus during successive phases of pregnancy.

The presence of a choriothete in *Hippobosca* is of interest in that it provides further evidence of the close relationship which, according to Bequaert (1953), subsists between this group and the tsetse flies.

5. The Milk Gland.

Working with *G. pallidipes* Austen, it has been possible to confirm the findings of Hoffmann (1953) with regard to the cycle of development of the milk glands. Milk secretion is restricted to a short period during the early part of pregnancy, feeding being limited to the first and early second instar larva.

With respect to the mode of feeding it is clear, as Hoffmann states, that the mouth of the larva is too small to encompass the whole of the uterine papilla. The latter, indeed, is laterally connected throughout its extent to the dorsal wall of the uterus and it is only in sagittal sections, as figured by Roubaud (1909) and Hoffmann (1953), that it appears to project freely from its roof. The papilla is, in fact, simply a thickening of the roof of the uterus at its junction with the oviduct. The term " teat " which has been applied to it is thus anatomically a misomer and might well be eschewed in view of the implications it carries with regard to the mechanism of feeding.

Examination of our preparations have led us to believe that the secretions of the milk gland are poured freely into the uterus, from which the larva recovers them by suction. The rhythmic contractions of the pharynx are well suited to this purpose ; they have been observed to comprise a lowering of the floor of the pharynx, the extent of the movement being greatest posteriorly and negligible near the oral aperture.

Two preparations have been examined which show that feeding has occurred

in the late first instar ; at this stage of development the mouth is largely blocked by the egg tooth and the possibility of the pharynx being pressed freely against the opening of the milk gland, as recorded by Hoffmann (1953), is precluded.[2]

Summary.

Degenerative changes of the choriothete result in its reduction from a massive musculo-glandular structure to a single layer of glandular cells in the course of each pregnancy.

Only the chorion and the first larval exuvium are removed by the choriothete. The second instar skin is shed independently of this organ.

A choriothete similar in structure and developmental cycle to that of the tsetse flies occurs in *Hippobosca longipennis* Fabricius.

Results suggest that there is no association between the mouth of the larva and the milk gland papilla, but rather that secretions are poured freely into the uterus from which the larva sucks them up.

Acknowledgments.

Our thanks are due to Mr. C. J. Webb for the production of the photomicrograph ; to Mr. Yahya Mohamed for skilful preparation of histological material ; and to Mr. R. D. Rennison for the larvae of *G. palpalis*.

References.

Bequaert, J. C., 1953, The Hippoboscidae or louse flies (Diptera) of mammals and birds. Part I. Structure, physiology and natural history. *Ent. amer.* **32** : 1–442.

Bursell, E., 1955, The polypneustic lobes of the tsetse larva (*Glossina*, Diptera). *Proc. roy. Soc.* (B) **144** : 275–86.

Burtt, E. and Jackson, C. H. N., 1951, Illustrations of tsetse larvae. *Bull. ent. Res.* **41** : 523–527.

Hoffmann, R., 1953, Zur Fortpflanzungsbiologie und zur intrauterinen Entwicklung von *Glossina palpalis*. *Acta trop., Basel*, **11** : 1–57.

Jackson, C. H. N., 1948, The eclosion of tsetse (*Glossina*) larvae (Diptera). *Proc. R. ent. Soc. Lond.* (A) **23** : 36–38.

Newstead, R., Evans, A. M. and Potts, W. H., 1924, *Guide to the study of tsetse flies*. Liverpool.

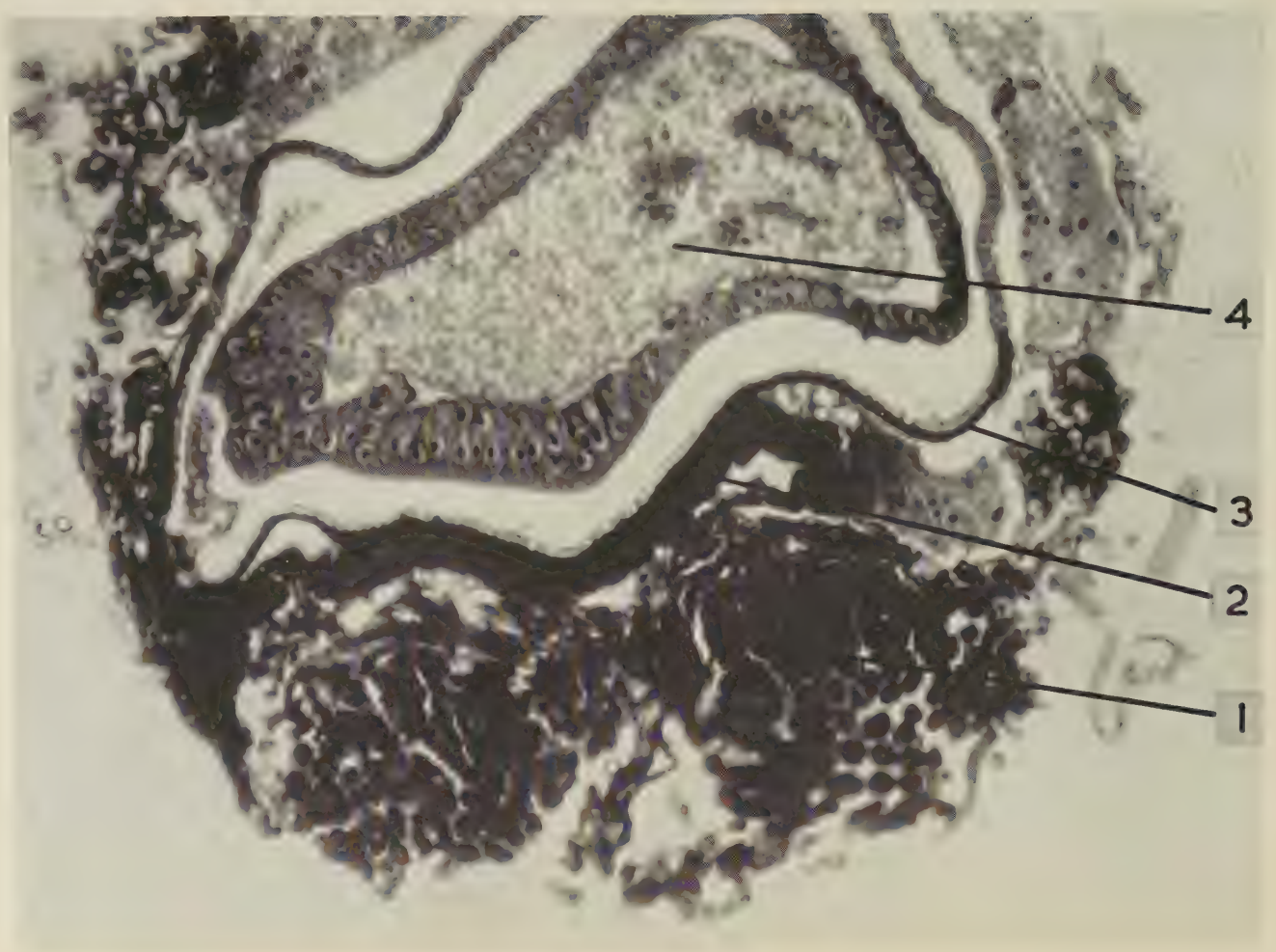
Roubaud, E., 1909, La *Glossina palpalis*, etc. Thesis No. 1344, Paris University. (Extract from *Rapport de la Mission d'études de la maladie du sommeil au Congo Français* (1906–1908), by G. Martin, Leboeuf, and Roubaud. Paris, Masson.

[2] Hoffmann (1953) was unable to find the well-developed egg tooth which is present in first instar larvae of *G. palpalis*, as in all the other species studied.

PLATE I.

Transverse section of the uterus of *Hippobosca longipennis* Fabricius showing the choriothete and embryo.

(1) Muscles of the choriothete : (2) Glandular epithelium. (3) Chorion. (4) Embryo.



Transverse section of the uterus of *Hippobosca longipennis* Fabricius.

ON THE INCREASE IN LINEAR SIZE DURING GROWTH IN *LOCUSTA MIGRATORIA* L.

By Kenneth U. Clarke.

(*Department of Zoology, University of Nottingham.*)

Introduction.

Przibram and Megusar (1912) on *Sphodromantis*, and Eidmann (1924) and Teissier (1931) on *Dixippus* have shown that increase in linear size in these animals occurs only at an ecdysis. Measurements made by other workers on other insects tend to confirm this, and it appears to be fairly generally accepted as the typical manner of growth in size of most insects. Insects which increase in size during a stadium, as well as at an ecdysis, are, as pointed out by Teissier (1931), those in which the exoskeleton is not typically developed. Observations on the changes in body volume that occurred during the growth of the locust showed that it increased during a stadium as well as at an ecdysis, the amount of increase being approximately equal in each case. As this necessarily implies changes in linear size during the stadium and, as the locust is an insect with a typically developed exoskeleton, measurements were made with a view to the further study of this phenomenon. An analysis of these measurements has shown that increase in linear size in this typical insect is rather more complex than previous observations have suggested.

Material and technique.

The insects used were females of *Locusta migratoria migratorioides* (R. and F.), populations of which were supplied by the Anti-Locust Research Centre, London.

The animals were reared in an insectarium at a temperature of 28° C. and a relative humidity of 70 per cent. Abundant food was always available to them. The lighting of the insectarium was controlled so as to give alternate periods of 12 hours light and 12 hours dark. The introduction of fresh food each morning caused the humidity to rise to 80 per cent. and provided a region of high humidity (90 per cent.) into which the locusts could move.

Measurements were made immediately before and after an ecdysis (intervals between these measurements are given in Table I) and at the beginning and end of a stadium. Twelve individuals were studied for each stadium and its subsequent ecdysis.

The following measurements were made at each observation : (1) the length of the hind femur and the length of the pronotum as specified by Uvarov (1921) ; (2) the length of the thorax measured between the anterior edge of the pronotum and the anterior edge of the tympanal depression (Albrecht, 1953) ; and (3) the length of the abdomen from the posterior edge of the tympanal depression to the base of the cercus. Measurements (2) and (3) were made on the right-hand side of the animal. All linear measurements were made in

millimetres and were accurate to 1 per cent. of their value. The weight of the animal in milligrams was also measured and this, too, was accurate to 1 per cent. of its value.

Results.

From these measurements for each individual Brook's ratio

$$\frac{\text{final measurement—initial measurement}}{\text{initial measurement}}$$

was calculated for each pair of observations. The mean of these ratios for each stadium and each ecdysis is given in Table I.

Table I.—*Brook's ratio for changes in linear size occurring during a stadium and at an ecdysis.*

Stage.	Interval between observations in hours.	Weight.	Length.			
			Hind femur.	Abdomen.	Pronotum.	Thorax.
1st stadium . .	115·00	+2·007	0·0	+0·610	0·0	+0·321
1st ecdysis . .	11·00	−0·068	+0·483	+0·043	+0·904	+0·441
2nd stadium . .	119·00	+1·638	0·0	+0·528	0·0	+0·209
2nd ecdysis . .	13·30	−0·058	+0·405	+0·053	+0·813	+0·600
3rd stadium . .	171·00	+1·260	0·0	+0·593	0·0	+0·106
3rd ecdysis . .	12·15	−0·048	+0·390	+0·039	+0·507	+0·331
4th stadium . .	222·30	+1·340	0·0	+0·501	0·0	+0·121
4th ecdysis . .	08·30	−0·082	+0·416	+0·046	+0·387	+0·272
5th stadium . .	310·45	+1·558	0·0	+0·405	0·0	+0·093
5th ecdysis . .	10·00	−0·086	+0·367	+0·039	+0·001	+0·245

The ratios were used to estimate the probable changes in linear size which each structure measured could be expected to undergo during the growth of the locust from hatching from the egg to the adult stage. At the moment of hatching the animal was assumed to weigh 15 mg., and to have a hind femur 4 mm. long, with the abdomen, thorax and pronotum 3·5, 1·2, and 1·3 mm. in length respectively, these being the mean values observed for 12 individuals immediately after hatching. The value for each variable given above was multiplied by its appropriate ratio given in Table I for the first stadium. This gave the increase in these values that would occur in the first stadium and which, when added to them, gave their size at the end of this time. By repeating this procedure, using the ratios given in the Table, the sizes of these structures at the beginning and end of each stadium were calculated. The results are illustrated in fig. 1.

A comparison of the ratios obtained for changes in weight during a stadium and at an ecdysis showed that this factor increased in the former and decreased in the latter period. The amount of increase was greatest for the first stadium (2·007), least for the third (1·260) and increased again for the fifth (1·558). The ratio of weight loss at each ecdysis was the same, being 0·068 of the previous weight of the animal.

The length of the hind femur and of the pronotum increased only at an ecdysis, both remaining constant in size during a stadium. At successive

ecdyses the hind femur showed a fairly constant increase in size of about half its initial length. The pronotum, however, showed its greatest increase (0·904) at the first ecdysis; thereafter this value decreased, being zero at the fifth ecdysis.

The length of the abdomen increased both during a stadium and at an ecdysis. During a stadium the increase was greatest (0·610) for the first, and least (0·405) for the fifth instar. Although at each ecdysis there was a large increase in size with the actual casting of the skin and the hardening of the cuticle, when the animal relaxed the abdomen showed only a slight increase (0·045) in size over its initial length.

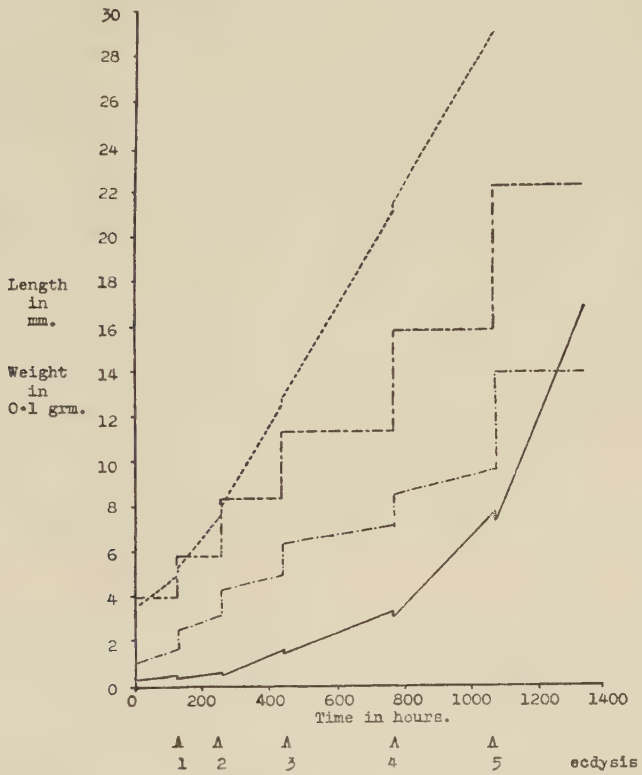


FIG. 1.—The patterns of growth in linear size that certain structures in an individual locust may be expected to undergo between hatching and the adult instar. ———— weight; — · — · — length of thorax; — — — length of hind femur; – – – – – length of abdomen. Changes in length of the pronotum are not shown; they are similar to those of the hind femur but there is no increase at the fifth ecdysis.

The length of the thorax also increased during a stadium and at an ecdysis. The amount of increase during a stadium was most (0·321) for the first and least (0·093) for the fifth instar. At an ecdysis the change was greatest at the second (0·600) and least at the fifth (0·245). A comparison of these two sets of ratios shows that the increase in the stadium was always less than that at an ecdysis, this difference being less in the earlier than in the later stages.

DISCUSSION.

The structures examined above show patterns of increase in linear size which can be related to the complexity of the region lying between the points of measurement. Simple sclerotic plates, such as the pronotum and the hind femur, show changes in size only at an ecdysis. Structures such as the thorax, which are sheathed mainly in sclerotic plates and have little intersegmental membrane, show a size increase during a stadium as well as at an ecdysis. Finally, in the abdomen, in which the sclerotic plates and the intersegmental membranes occupy approximately equal areas of the exoskeleton, increase in linear size occurs mainly during the stadium and the increase at an ecdysis is small. This relationship allows the increase in linear size which occurs during a stadium to be harmonised with the essence of the classical view that growth of linear dimensions occurs only at an ecdysis.

There appear to be no exceptions to the statement that sclerotic plates increase in their dimensions only at an ecdysis, and studies on the histology of moulting suggest that this is true also of the intersegmental membranes. Measurements made on the intersegmental membranes between the first and second abdominal segments of the locust confirm that these increase in size only at an ecdysis. Strictly speaking, neither the sclerotic plates nor the intersegmental membranes ever increase in size; they are replaced by ones of larger size at a moult.

That this remains true in spite of the changes in linear size recorded during a stadium is due to the folding of the intersegmental membranes under the sclerotic plates immediately after a moult, and their subsequent unfolding during the next stadium. In tagmata such as the thorax, where the intersegmental membranes are small, little change in size will occur during a stadium. Where, as in the abdomen, the membranes form a larger part of the surface area their growth at an ecdysis may be largely masked by their folding under the sclerotic plates immediately ecdysis is concluded. In the following stadium the unfolding of these membranes will allow a considerable increase in linear size to occur.

In the case of *Dixippus*, used by Eidmann (1924) and Teissier (1931), the insect is an elongate creature with most of its body surface occupied by sclerotic plates, the intersegmental membranes being small. Growth in this animal is controlled by these sclerotic plates, so that increase in linear size will only take place at an ecdysis. In other insects such as *Jalysus spinosus* (Readio, 1923), larvae of *Dytiscus* (Blunck, 1923) and *Nannothemis bellis* (Calvert, 1929), where the proportions of intersegmental membrane to sclerotic plate are similar to those in the locust, increase in linear size has been found to occur during the stadium as well as at an ecdysis. In these insects the increase in linear size is divorced from the real growth in size of the exoskeleton.

Summary.

Measurements were made of the changes in linear size of a number of structures during the growth of the locust.

These showed that linear size increased during a stadium as well as at an ecdysis providing the structure measured contained both sclerites and intersegmental membranes.

In these structures the increase in linear size does not reflect true growth. The folding of intersegmental membranes beneath the sclerites allows, by their unfolding during the following stadium, the increase in linear size that has been observed to occur.

The dominant type of growth shown by the whole animal can be related to the proportions of sclerotic plate to intersegmental membrane in its exoskeleton.

References.

Albrecht, F. O., 1953, *The Anatomy of the Migratory Locust.* University of London, The Athlone Press.

Blunck, H., 1923, Die Entwicklung des *Dytiscus marginalis*. *Z. wiss. Zool.* **121** : 171–391.

Calvert, P. P., 1929, The different rates of growth among animals with especial reference to the Odonata. *Proc. Amer. Phil. Soc.* **68** : 227–274.

Eidmann, H., 1924, Untersuchungen über Wachstum und Hautung der Insekten. *Z. Morph. Ökol. Tiere* **2** : 566–610.

Przibram, H. and Megusar, F., 1912, Wachstumsmessungen an *Sphodromantis bioculata* Burm. Lange und Masse. *Arch. EntwMech. Org.* **34** : 680–741.

Readio, P. A., 1923, The life history of *Jalysus spinosus* (Say). *Canad. Ent.* **55** : 230–236.

Teissier, G., 1931, Recherches morphologiques et physiologiques sur la croissance des Insectes. *Trav. Sta. biol. Roscoff.* **9** : 29–238.

Uvarov, B. P., 1921, A revision of the genus *Locusta* L. with a new theory as to the periodicity and migrations of locusts. *Bull. ent. Res.* **12** : 135–163.

THE RETROCEREBRAL ENDOCRINE ORGANS OF THE LARVA OF *PROTOPHORMIA TERRAE-NOVAE* ROBINEAU-DESVOIDY (DIPTERA: CYCLORRHAPHA).

By Alastair Fraser.

(Department of Zoology, University of Glasgow.)

I. Introduction.

Descriptions of the ring of Weismann (1864) in the larvae of Calliphorinae (Diptera) have been given by Lowne (1890), Burtt (1937), Thomsen, E. (1941), Day (1943), Vogt (1943), Thomsen, M. (1951) and Possompès (1953). Fraser (1955) commented on points on which these authors disagree and indicated that the anatomy of the retrocerebral endocrine complex of the larva of *Protophormia terrae-novae* R-D. differs sufficiently from that known in other Calliphorinae to warrant detailed description. It has been decided to adopt Wigglesworth's (1952) term " thoracic gland " for the large cell component of Weismann's ring in preference to other current synonyms.

II. Material and Technique.

Third instar larvae taken before and after the cessation of feeding were used in this investigation. Larvae were dissected under a low power binocular in Ringer's solution. The innervation of the corpus cardiacum was studied by vital staining with 0·1 per cent. methylene blue in Ringer's solution. The tracheal systems were observed in dissections of anaesthetised larvae before and after methylene blue vital staining and in whole fresh organs mounted in glycerine. Material required for sectioning was fixed in Bouin's fluid. Steedman's (1947) ester wax was the embedding medium used, sections being cut at 6μ and stained with haemalumeosin, iron haematoxylin and chrome haematoxylin-phloxin by Gomori's technique (1941).

III. Anatomy of the Retrocerebral Organs.

The single corpus cardiacum is incorporated in the ventral wall of the aorta above the larval brain. It is an elongate body receiving near its posterior limit a branch from the recurrent nerve. M. Thomsen's identification of the swelling in the recurrent nerve, from which this branch arises, as the hypocerebral ganglion is accepted. Anterior to this the corpus cardiacum receives a pair of nerves arising from the posterior inner faces of the cerebral hemispheres close to the insertions of the cerebral tracheae. At the point of emergence of each nerve there also arises a pair of muscular connective strands, the one passing forward alongside the recurrent nerve to meet the junction of the

frontal sac and the functional pharynx, the other passing upwards alongside the nerve to the corpus cardiacum. This latter strand is attached to the nerve for most of its length but they part before the nerve enters the corpus cardiacum and the strand continues upwards through the gap between the ring and the aorta to join the mid-lateral wall of the aorta. A second pair of connectives link the corpus cardiacum to the brain. These emerge from the hind face of the pars intercerebralis and, after each has divided into two branches, join the ventral surface of the aorta at the anterior end of the corpus cardiacum. The author, in accepting that these anterior connectives were also nerves, was in agreement with the findings, in *Calliphora*, of Burtt and Thomsen, M., and in disagreement with Possompès (1953). Further investigation has now proved that these are muscle strands. In order to demonstrate these very slender structures by vital staining or to treat the brain and neighbouring organs with fixative, before removal for sectioning, the technique employed involved an abnormal stretching of the aorta and of the connectives to the brain. As a result only a longitudinal fibrillation was apparent in the anterior pair, highly comparable to that seen in the posterior connectives. Dissimilarities are also masked by the muscular strands intimately associated with each of the true nerves to the corpus cardiacum. The contention of Cazal (1948), supported by Possompès (1953), that there exists only one pair of nerves of the corpus cardiacum in dipterous larvae, therefore stands.

The large cells which, in other Calliphorinae, form a continuous ring around the aorta, form two separate thoracic glands in *P. terrae-novae*. Ventrally these are attached to each side of the corpus cardiacum above the point of entry of the branch from the recurrent nerve. Dorsally they overlie the corpus allatum and each thoracic gland forms an anterior prolongation uniting with the cephalo-pharyngeal band. They are otherwise free of the aorta (fig. 1).

The paired origin of the corpus allatum is evident. It is a V-shaped structure formed of two lobes uniting anteriorly where the corpus allatum overlies the posterior limit of the cephalo-pharyngeal band (fig. 2). Behind this point the separate lobes are supported by the transverse anastomosing trachea (fig. 3). The position of the anterior ends of the thoracic glands relative to the corpus allatum can be seen in figures 2 and 3.

IV. Tracheal Supply to the Retrocerebral Organs.

Each cerebral hemisphere receives a trachea branching from the longitudinal trunk of its side. Just anterior to the brain there is a transverse anastomosing trachea linking these cerebral tracheae. It passes over the aorta, uniting with the dorsal wall of the latter (fig. 3), and supports the posterior lobes of the corpus allatum. The thoracic glands are not in contact with the cerebral tracheae in this species apart from several very fine connective strands.

A trachea leaves the longitudinal tracheal trunk of each side at the level of the first abdominal segment and sends branches to the proventriculus, salivary glands, enteric caeca, fat body and malpighian tubules. The one on the right also has branches to the proventricular ganglion and the recurrent nerve, and a single branch passing forward (fig. 1). Very rarely this single branch comes

from the corresponding position on the left. Beneath the corpus cardiacum this divides into four tracheae, one going to each thoracic gland and one to each side of the corpus cardiacum. Minor variations occur at this level but it is usually the trachea to the right thoracic gland which sends tracheoles into the hypocerebral ganglion.

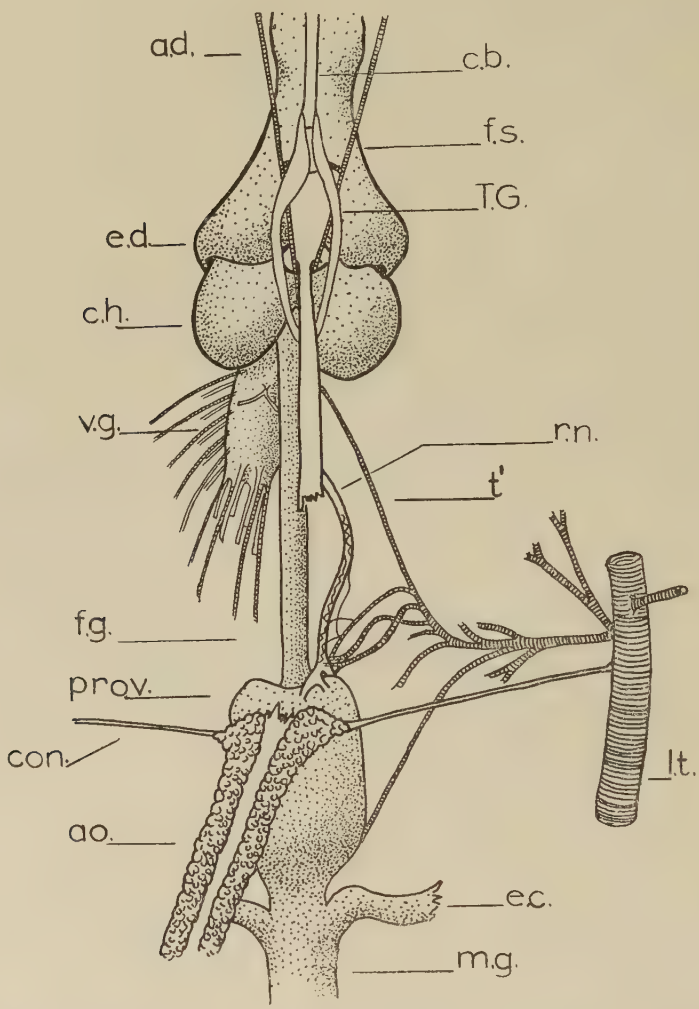
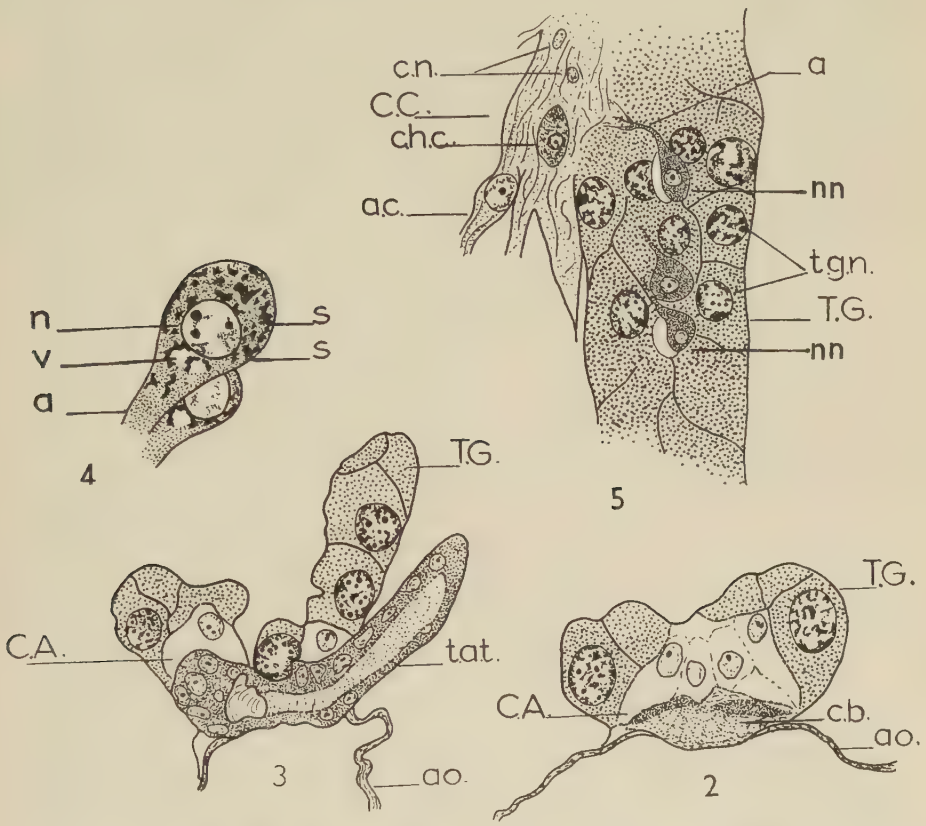


Fig. 1.—Diagram showing the derivation of the tracheal supply to the retrocerebral organs, proventriculus, etc. *c.h.*, cerebral hemisphere; *v.g.*, fused ventral ganglia; *f.g.*, fore gut; *prov.*, proventriculus; *e.c.*, enteric caecum; *m.g.*, mid gut; *ao.*, aorta; *con.*, lateral connective strands linking aorta to longitudinal tracheae; *l.t.*, longitudinal tracheal trunk; *t'*, single tracheal branch passing forward; *r.n.*, recurrent nerve terminating posteriorly in the proventricular ganglion; *T.G.*, thoracic gland; *c.b.*, cephalo-pharyngeal band; *e.d.*, eye disk; *a.d.*, antennal disk; *f.s.*, frontal sac.

V. Histological Observations.

In sections of brains of larvae, in the post-feeding prepupation phase, the neurosecretory cells, from which it may be assumed the nerves to the corpus cardiacum arise, are readily identified after staining with acid chrome-haematoxylin after permanganate oxidation. They can also be distinguished at this stage in the living brain, forming a scattered group on either side of the



Figs. 2–5.—(2) Transverse section of corpus allatum (1). (3) Transverse section of corpus allatum (2). (4) Neuro-secretory cells in the brain of *Protophormia terrae-novae* R-D. (5) Section at the junction of thoracic gland and corpus cardiacum.

C.A., corpus allatum ; *C.C.*, corpus cardiacum ; *T.G.*, thoracic gland ; *a*, axon ; *a.c.*, anterior connective to the C.C. ; *ao*, aorta ; *c.b.*, cephalo-pharyngeal band ; *ch.c.*, "chromophile" cell ; *c.n.*, " chromophobe " cell nuclei ; *n*, nucleus ; *nn*, neurons located in the thoracic gland ; *s*, secretory " granules " ; *t.a.t.*, transverse anastomosing trachea ; *t.g.n.*, thoracic gland cell nuclei ; *v*, vacuoles.

pars intercerebralis. Fig. 4 shows a typical neurosecretory cell with the cytoplasm charged with particles of varying size of a product coloured a distinctive blue by the above stain. It proved impossible to trace the axons of these neurons into the nerves. Axonal transport of the neurosecretory product was not observed but particles of it were detected in the corpus cardiacum in

some sections. A number of vacuoles are usually evident in these cells, presumably representing the space occupied by material removed during the fixation, embedding or staining processes, or uncoloured by the stains used. The possibility that this is some lipid substance suggests itself. A fuller cytochemical study of these cells is in progress.

The corpus cardiacum, as expected, was found to contain nuclei of the two types of cells denoted by Cazal (1948) as " chromophile " and " chromophobe ". The nuclei of the latter are abundant, there being more than a hundred in a mature larva, and are more concentrated in the posterior part of the organ. They range in size from 4·5μ to 16μ in diameter, with a mean size of 7·5μ, have a single nucleolus, are relatively poor in chromatin and, as M. Thomsen notes, they appear similar to nuclei found in the hypocerebral ganglion. These cells appear to form a syncytium. The chromophile cells are few in number and are arranged in two lines corresponding to the two corpora cardiaca now fused. Each cell lies embedded in the syncytium, and is elongated in the long axis of the aorta, a typical one at this stage measuring 18μ × 10μ with a round nucleus about 7μ in diameter. As others have observed, some of these cells appear in sections to have a polygonal form but this may be a fixation artefact, as vitally stained cells have a more regular ellipsoid outline. There is no evidence that these cells possess axons or dendrites. Several workers have noted cells in the thoracic glands, other than the large cells characteristic of these organs, which they consider similar to these chromophile cells. In each thoracic gland there are four cells which bear a superficial resemblance to these but which are apparently neurons, each with a single axon whose course can, in some cases, be traced as far as the corpus cardiacum (fig. 5). These cells are pyriform and have a nucleus of average diameter 7·5μ. Their cytoplasm has slightly different staining properties from that of the chromophile cells. The space beside the two cells depicted in the figure is a regular feature but is probably a fixation artefact.

The location of the corpus allatum has already been described. There are about twenty-eight cells in this organ with subspherical nuclei 10–14μ in diameter and often showing a pair of nucleoli. The existence of nerves to the corpus allatum was not demonstrable by the techniques used.

The large thoracic gland cells do not differ in detail from those described in related species. The nuclei increase in size between the time of cessation of feeding and pupation, and at the latter time may exceed 25μ in diameter.

VI. Discussion.

The possession of symmetrical paired thoracic glands is a remarkably primitive feature to be found in a member of the Cyclorrhapha. It is known in some Nematocera (Possompès, 1948 ; Thomsen, M., *loc. cit.*) but not in any of the higher Diptera so far described. Tracheation of these organs (apart from simple superficial contact with the cerebral tracheae) is unknown in Cyclorrhapha but occurs in other Diptera. Possompès, from his observations in *Chironomus plumosus*, named them the " peritracheal glands ". The asymmetry of the tracheal supply to these glands in *Protophormia* is, however, unique and suggests a secondary adaptive feature. The purpose of these trachea may be to " accelerate " the activity of the thoracic glands and of the

corpus cardiacum, the duration of the phase between cessation of feeding and puparium formation being, in this species, only one third as long as that in the related genera *Lucilia* and *Calliphora* (Cochrane, *personal communication*).

The form of the corpus allatum might be likened to that of a crescent with the horns directed towards the rear. M. Thomsen describes the organ as crescent shaped in *Thereva sp.* (Diptera-Brachycera), but in this animal it is the posterior component of the retrocerebral complex, and the horns of the crescent point forwards. The anterior ends of the corpus allatum in *Thereva* are connected to the thoracic glands which pass downwards and forwards to unite below the aorta. In Thomsen's description the location of the corpus cardiacum is not clear but he notes a single pair of nerves from the brain to the ventro-median part of the " ring ". It is apparent that in the rearwards shift of the brain in the larvae of Cyclorrhapha the relative positions of the components of the complex have been altered. The corpus allatum in *Protophormia* has become the anterior organ and the thoracic glands pass downwards and backwards.

While such internal anatomical details may be of doubtful taxonomic value, the divergence of the arrangement in *Protophormia* from that known in other members of the same sub-family suggests that an extension of this study to other Cyclorrhapha might be rewarding.

VII. Acknowledgments.

I am indebted to Dr. A. R. Hill and Mr. D. G. Cochrane of this Department for their interest and helpful criticism and wish to thank Mr. W. F. Smith for technical assistance.

VIII. Summary.

The anatomy of the retrocerebral endocrine organs of *Protophormia terrae-novae* R.-D. is described in detail, features emphasised being the existence of only one pair of nerves to the corpus cardiacum, the existence of two thoracic glands and consequent absence of a complete circum-aortal ring, and the presence of a bilobed corpus allatum. An account is given of the asymmetrical tracheal supply to the thoracic glands and corpus cardiacum and histological observations include a description of the neurosecretory cells of the brain and a claim that the " chromophile " cells found in the thoracic glands are nerve cells. The significance of certain of these observations is discussed.

IX. References.

Burtt, E. T., 1937, On the corpora allata of dipterous insects. *Proc. roy. Soc.* (B) **124** : 13–23.

Cazal, P., 1948, Les glandes endocrines rétro-cérébrales des Insectes. *Bull. biol.*, Suppl. **32** : 1–227.

Cochrane, D. G., *Unpublished records.*

Day, M. F., 1943, The homologies of the ring gland of Diptera Brachycera. *Ann. ent. Soc. Amer.* **36** : 1–10.

Fraser, A., 1955, Location and innervation of the corpus cardiacum in the larvae of some Calliphorinae (Diptera). *Nature, Lond.* **175** : 817.

Gomori, G., 1941, Observations with differential stains on human Islets of Langerhans. *Amer. J. Path.* **17** : 395.

Lowne, B. T., 1890–95, *The anatomy, physiology, morphology and development of the Blow-fly* (Calliphora erythrocephala). 2 vols., 778 pp., London.

Possompès, B., 1948, Les corpora cardiaca de la larve de *Chironomus plumosus* I. *Bull. Soc. zool. Fr.* **76** : 202–206.

——, 1953, Recherches expérimentales sur le déterminisme de la métamorphose de *Calliphora erythrocephala* Mg. *Arch. Zool. exp. gén.* **89** : 203–364.

Steedman, H. F., 1947, Ester wax, a new embedding medium. *Quart. J. micr. Sci.* **88** : 123.

Thomsen, E., 1941, Ringdrüse und Corpus allatum bei Musciden. *Naturwissenschaften* **29** : 605–606.

Thomsen, M., 1951, Weismann's ring and related organs in larvae of Diptera. *Biol. Skr.* **6** : 1–32.

Vogt, M., 1943, Zur Kenntnis des larvalen und pupalen corpus allatum von *Calliphora*. *Biol. Zbl.* **63** : 56–71.

Weismann, A., 1864, Die nachembryonale Entwicklung der Musciden nach Beobachtungen an *Musca vomitoria* und *Sarcophaga carnaria*. *Z. wiss. Zool.* **14** : 187–336.

Wigglesworth, V. B., 1952, The thoracic gland in *Rhodnius prolixus* (Hemiptera) and its role in moulting. *J. exp. Biol.* **29** : 561–570.

OBSERVATIONS ON CASE-BUILDING BY THE LARVAE OF *LIMNEPHILUS POLITUS* McLACHLAN AND *L. MARMORATUS* CURTIS (TRICHOPTERA : LIMNEPHILIDAE).

By Hilmy M. Hanna.

(*Zoology Department, University of Manchester*).

Introduction.

Many observations on the different aspects of case-building by larvae of caddis flies have been published, but the sequence of events has been described for only a few species. Marshall and Vorhies (1905) observed that *Platyphylax designatus* Walker used its mandibles in handling sand grains for case-building and would repair damage done to the anterior end of the case. Bierens de Haan (1922) described the manner in which *Limnephilus marmoratus* Curtis wrapped the materials around itself to build its case. Gorter (1929) made similar observations on *L. flavicornis* (F.). Neither Bierens de Haan nor Gorter, however, described the full sequence of events in case-building. Gorter (1931) gave details of the construction of a provisional case, followed by a permanent one, by larvae of nine species of Limnephilids and two species of Leptocerids. Dembowski (1933) described the way in which *Molanna angustata* Curtis constructed its case in front of a heap of material which it had collected. Fankhauser and Reik (1935) observed that the larvae of *Neuronia postica* Walker constructed a rough preliminary sheath which was followed by a regular final case. Copeland and Crowell (1937) studied case-building by a *Limnephilus* species and a *Molanna* species. In view of the wide range of variation in the behaviour of the species of *Limnephilus*, it was unfortunate that these authors did not identify the species. Nielsen (1948) studied the case-building of five species of Hydroptilidae. Whitehead (1951) made observations on the increase in size of the larval cases of *Limnephilus vittatus* (F.). Maillet and Carasso (1952) described the case-building of *Triaenodes conspersa* (Rambur). The same authors (1954) also studied the case-construction of an unidentified species of *Setodes*.

A study of this review of literature shows the need for more observations on case-building. Furthermore, there has been no attempt to make a comparative study of the growth of larvae and cases. I have, therefore, made such a study in *L. politus* and *L. marmoratus*.

Material and Methods.

The larvae were collected from two open pools at Heaton Mersey near Manchester. Caseless larvae were provided with stalks of water plants, *Elodea* leaves, *Lemna* leaves, mollusc shells and sand grains. The larvae were observed carefully under a binocular microscope. Observations were made on both young and old larvae.

Details of the growth of the larvae and their cases were obtained by making monthly collections of about a hundred larvae over a period of one year.

Measurements were made to the nearest millimetre with the aid of a binocular microscope fitted with a squared eye-piece and the mean lengths of the larvae and their cases were calculated month by month.

In order to study the way in which the growth of the case takes place, a number of larval cases of various sizes were taken to pieces and the number of stalks, together with their lengths, was recorded.

Results.

Limnephilus politus MacLachlan.

The larva constructed a plate by secreting silk over a mass of varied materials which it had collected with the claws of the pro- and mesothoracic legs. The larva then turned on to its back and the mesothoracic legs were stretched outwards as far as possible until they held the edges of the plate.

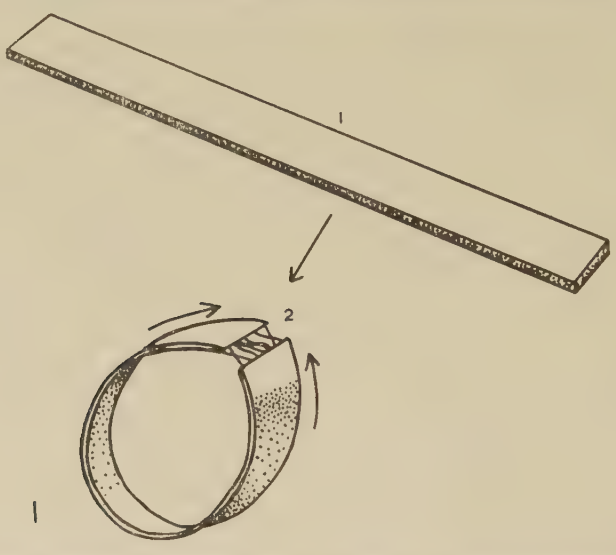


Fig. 1.—Diagram showing the construction of a belt by *Limnephilus politus* McLachlan.

The latter were then drawn towards each other (fig. 1). The head was moved to and fro and many silk threads were secreted and the two ends fastened together. The larva was now encircled by a small belt, which, by moving the abdomen backwards and forwards, was pushed backward over the thorax. The larva collected one stalk at a time and drew it towards the labium by means of the claws of the pro- and mesothoracic legs, covering it with silk secretion as the legs moved it up and down. A number of stalks were fixed obliquely and transversely at the anterior end of the belt. If the stalk was too long the larva would cut it with its mandibles. Small pieces of dead leaves and mollusc shells were also included in the construction of the case. From time to time the larva went inside to secrete more silk. As soon as the case was as long as the abdomen, the larva reversed itself inside and cut away the belt with its mandibles. Small pieces of material were then added at the posterior

end so that the posterior opening of the case became smaller. The larva continued to build at the anterior end. Young larvae appeared to be active during all the stages of case-construction and they built their cases in about three hours. Older larvae had periods of inactivity which lasted up to forty

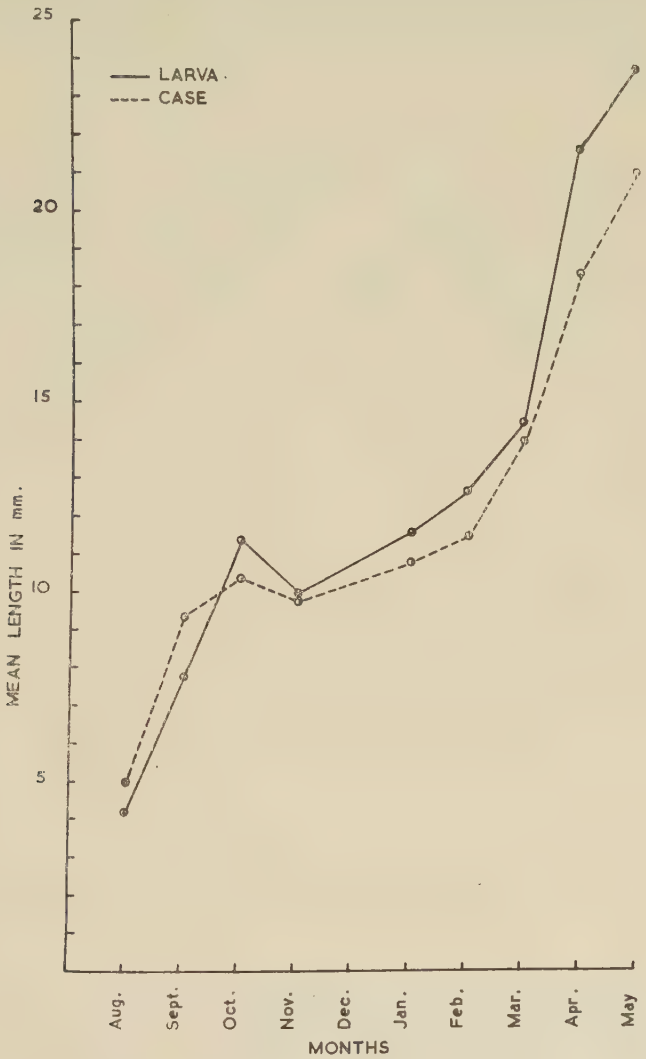


FIG. 2.—Monthly average length of larvae and cases of *Limnephilus politus* McLachlan.

minutes in some of the specimens, and they built their cases in two days. Larvae which were ready to pupate failed to build new cases although they tried to do so. The growth of the case took place by adding new material to the front end and cutting off the posterior end at intervals and it took place parallel with the growth of the larva (fig. 2). During those months of the year when the larvae grew rapidly, the enlargement of the case tended to lag

behind and it took as much as two months before the deficiency in the length of the case was made good.

There was little difference in the number of stalks used for the construction of cases measuring 4–8 mm. in length, but the average length of the stalks increased with the length of the case. In larval cases of more than 8 mm. in length, there was little increase in the mean length of the stalks used but the number increased with the length of the case.

Limnephilus marmoratus Curtis.

Although the larvae of this species built cases similar to those of *L. politus*, they started to do so in a completely different way. The larva secreted silk over a flattened mass of material which it had collected, thus forming a plate which extended beneath the abdomen. The larva then turned first on to one side and then on to the other, adding some stalks at right angles to the edges of the plate. Later the larva turned on to its back and added material to the roof, completing a square (fig. 3). The square was then slipped over the head

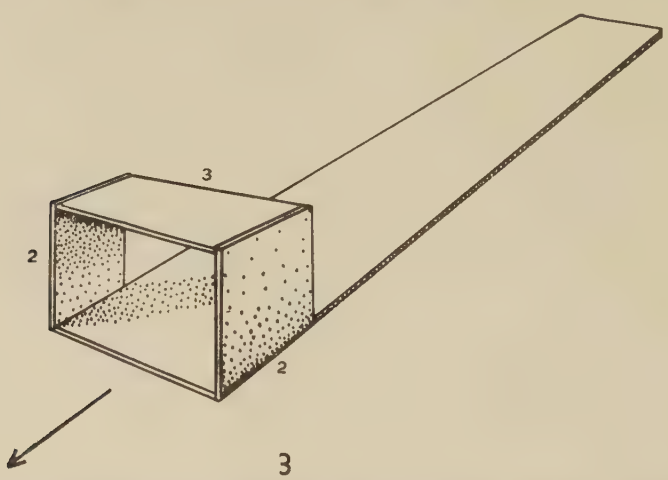


Fig. 3.—Diagram showing the construction of a ventral plate and square by *Limnephilus marmoratus* Curtis.

and more stalks were fixed to its anterior end. The stalks were held in the angle of the femora and tibiae. The stalks of the ventral plate became separated from one another after a considerable part had been constructed. The case was completed in much the same way as described for *L. politus*.

The growth of the case took place parallel with that of the larva (fig. 4). Between January and February the length of the larvae increased rapidly and this continued until the end of April, after which the growth rate gradually declined until pupation in May and June. The enlargement of the case lagged slightly behind the increase in the size of the larvae, although the difference between the size of the larvae and that of the cases gradually decreased between April and June ; it had not disappeared by the time the larvae pupated.

There was a linear relationship between the length of the case and the mean length of the stalks in cases ranging from 4–15 mm. in length. In cases over 15 mm. long, the length of the stalks used by the larvae showed a slight

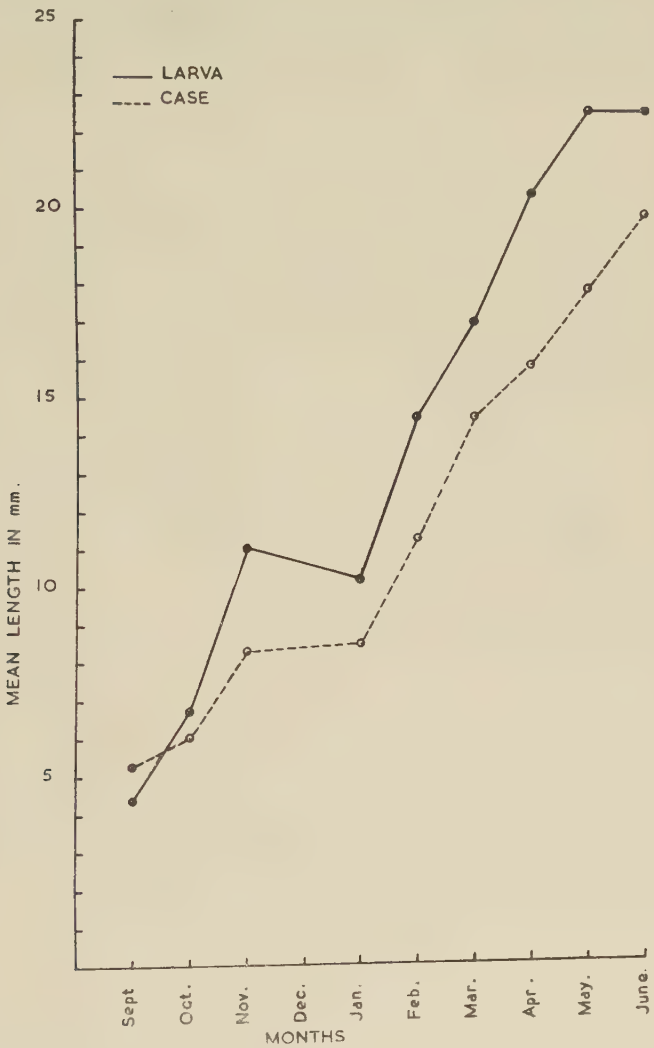


Fig. 4.—Monthly average length of larvae and cases of *Limnephilus marmoratus* Curtis.

decrease. In a similar way the number of stalks used increased with the length of the larval case in cases ranging from 4–14 mm. in length. In cases longer than this, the number of stalks showed a slight decrease. A comparison of small and large cases, however, showed that the thickness of the stalks increased with the length of the larval case.

Summary.

(1) A detailed study of case-building by larvae of *L. politus* and *L. marmoratus* showed that the former species started its case by constructing a belt, whereas the latter species constructed a ventral plate and square.

(2) The increase in size of the cases of both species was achieved by adding material to the front end and cutting from the posterior end.

(3) The growth of the case took place parallel with the growth of the larva.

References.

Bierens de Haan, J. A., 1922, Über den Bauinstinkt einer Köcherlarve (*L. marmoratus*). *Bijdr. Dierk.* **22** : 321–7.

Carasso, N. and Maillet, P., 1954, Reconstruction du fourreau larvaire chez un Trichoptère Leptoceridae appartenant au genre *Setodes*. *Ann. Sci. nat.* **16** (11) : 35–49.

Copeland, M. and Crowell, S., 1937, Observations and experiments on the case-building instinct of two species of Trichoptera. *Psyche, Camb. Mass.* **44** : 125–31.

Dembowski, J., 1933, Über die Plastizität der tierischen Handlungen. Beobachtungen und Versuche an *Molanna* Larven. *Zool. Jb.* **53** : 261–311.

Fankhauser, G. and Reik, L. E., 1935, Experiments on the case-building of the caddis fly larva *Neuronia postica* W. *Physiol. Zool.* **8** : 337–59.

Gorter, F. J., 1929, Experiments on the case-building of a caddis worm (*L. flavicornis*). *Tijdschr. ned. dierk. Ver.* **1** : 90–93.

—— 1931, Köcherbauversuche an Trichopterenlarven. *Z. Morph. Ökol. Tiere* **20** : 443–532.

Maillet, P. and Carasso, N., 1952, Reconstruction du fourreau larvaire chez un Trichoptère Leptoceridae *Triaenodes conspersa* (Ramb.). *Ann. Sci. nat.* **14** (11) : 473–90.

Marshall, W. S. and Vorhies, C. T., 1905, The repair and rebuilding of the larval cases of *Platyphylax designatus* Walker (Phryganidae). *Biol. Bull.* **9** : 232–44.

Nielsen, A., 1948, Post-embryonic development and biology of the Hydroptilidae. A contribution to the phylogeny of caddis flies and to the question of the origin of case-building. *K. danske vidensk. Selsk. Skr.* **5** : 1–200.

Whitehead, H., 1951, Note on the growth and development of a caddis fly larva, *Limnephilus vittatus*. *Naturalist, Lond.* **1951** : 13–15.

THE RELATION BETWEEN AGE AND COLD RESISTANCE IN TSETSE FLIES AND THE VALUE OF CHILLING WHEN TRANSPORTING TSETSE FOR EXPERIMENTS.

By G. F. Burnett.

(*Colonial Pesticides Research Unit, Arusha, Tanganyika.*)

Buxton (1955 : 221) summarises the information available on the effect on tsetse flies of exposure for short periods to temperatures below 13° C. Speaking of *Glossina tachinoides* at 0° C. he remarks " the after effects are curiously irregular, for after an exposure of a few minutes some flies die, but some recover after much longer exposures, such as 4 to 7 hours ", and the same might be said of several other species. An observation made during a field experiment suggested that the irregularity, and also the conflicting results obtained by different workers, was due to increased susceptibility in older flies and this has been followed up and confirmed in both laboratory and field.

The original experiment carried out at Urambo, Tanganyika Territory, involved transporting wild-caught *G. morsitans* (Westw.) to a central point, marking, releasing and recapturing them. In order to avoid depletion of their food reserves they were chilled to immobility (Webb, *quoted in* Jackson, 1952). The only references available at the time suggested that confinement for four hours at temperatures just above freezing would not harm the insects (Potts, 1933 ; Vanderplank, *unpublished*), and a preliminary test on five day-old laboratory-emerged *G. palpalis fuscipes* (Newst.) confirmed this. In the field all flies recovered their mobility on warming up but on some days numbers were later found dead in the release cage and recapture data indicated that there was further considerable delayed mortality. Such delayed mortality was found by Vanderplank with tsetse flies of several species including *G. palpalis fuscipes* and *G. morsitans*, which, when kept at 0° C., all recovered but were unable to feed even if they had been chilled for only a few minutes. Our wild flies were not exposed to temperatures below 1·5° C. but endured this for up to an hour. There was no significant difference in the recaptures of males of different hunger states (Jackson, 1933) or between males and females, but a much higher proportion of teneral (young) flies than of non-teneral was recaptured in the first four days after release—40 per cent. of the young flies compared with 20 per cent. of the old ones. It appeared that this might be due either to the superior resistance to cold of young flies or to the fact that they had not fed, for both Potts (1933) and Vanderplank (*unpublished*) attributed delayed mortality to digestive upsets. Both theories have been tested in the laboratory with *G. palpalis fuscipes* emerged from pupae collected from near Lake Victoria, and the effect of age checked in the field with wild *G. morsitans*. The times and temperatures used in both cases are somewhat miscellaneous since the prime reason for the experiments was to find a satisfactory method for use in the type of dispersal experiment which suggested the work in the first place.

Proc. R. Ent. Soc. Lond. (A) 32. Pts. 4–6. (June, 1957).

Laboratory Tests.

Method.

The tsetse used had emerged in the laboratory from wild pupae collected near Entebbe, Uganda. The pupae were kept in a sensibly constant temperature of 27° C. and the adults after emergence were kept in Bruce boxes over water, at laboratory temperature. This varied from 20–25°C. during the period concerned. Flies were offered rabbits as food every day from the day of emergence but were not fed on the day of an experiment until after they had been used and then allowed about an hour to warm up. They were kept in the laboratory after experiments, for which they were confined two at a time in 3 in. × 1 in. glass tubes plugged with cotton wool. The number available was limited.

The temperature chamber was a vacuum flask containing (*a*) ice wrapped in cloth gauze ; (*b*) water ; or (*c*) ice with sufficient water to come half-way up the tubes. The last procedure had been used in the field and cooled the tubes in about seven min. to 2·5° C. Subsequent fall in temperature was slow, reaching about 1·5° C. in three hours. The other two treatments were possible alternative field methods. When the tubes stood on ice without water they cooled very slowly, reaching 10° C. from room temperature in about 15 min., about 7·5° C. in one hour and 5–6° C. in three hours. Water alone was used at 9–10° C. with the tubes immersed for half their lengths. They were rapidly cooled to water temperature, which was maintained as necessary by addition of ice-water. Temperatures were taken with a thermometer inserted into one of the tubes, its bulb wrapped with metal foil and in close contact with the wall of the tube.

Results.

The effect of cooling on flies of various ages is shown in Table I. At all temperatures all flies were immobile but in ice-plus-water they were completely paralysed and fell to the bottom of the tubes. All specimens appeared to recover on returning to room temperatures (23–25° C.). Approximately equal numbers of the sexes were used but, to avoid complicating the table, they are not enumerated separately.

Discussion.

There was no marked difference in the resistance of the two sexes to the immediate effects of cooling but there was an indication of higher subsequent mortality in the males ; the difference was small. In a wild population, so far as is known, the average age of the males is less than the females (Jackson 1941) and the lower susceptibility of the males due to their youth will outweigh the difference due to sex ; the females will suffer greater proportionate mortality in nature. There is a progressive and rapid loss of resistance to cold with increasing age, in both sexes. The viability of teneral flies is quite unaffected by the most rigorous treatment used but seven day-old tsetse lost 58 per cent. of their numbers within two days of exposure, 10-day-old flies were reduced by 63 per cent. in one day and two-week-old insects were all dead within a day, although exposed for only one hour instead of three.

The use of ice alone in the flask gave a more variable temperature, falling to 5–6° C. Sixteen-day-old tsetse subjected to this suffered 80 per cent. mortality

within a day, but the survivors were thriving a week later. Although five-day-old flies all survived for three days their losses in the next four days were higher than usual in controls. The mildest treatment employed (9–10° C. for 3–4 hours) was completely harmless to even the oldest flies but appears to have reduced the viability of five-day-olds. These were exposed for a rather longer period and may have included weaklings which had already been lost by the batch of old flies during their longer period in the laboratory (compare control deaths in Table I).

TABLE I.

Test no.	Age (days).	Treatment.	Number of flies.	Number dead in each 24 hr. after treatment. Day. 1.	2.	3.	4.	5.	6.	7.	Total.	Remarks.
1	1 (unfed)	Ice and water for 1 hr. (min. temp. 2·5° C.)	4	*Nil*	*Nil*	*Nil*	*Nil*	*Nil*	*Nil*	*Nil*	*Nil*	All fed and meals digested.
		Ice and water for 3 hr. (min. temp. 1·2° C.)	6	,,	,,	,,	,,	,,	,,	,,	,,	
	2	Ice and water for 1 hr. (min. temp. 2·5° C.)	6	,,	,,	,,	,,	,,	,,	,,	,,	* Died after gorging—not unusual in laboratory.
	2	Ice and water for 3 hr. (min. temp. 1·5° C.)	6	,,	,,	,,	,,	,,	,,	1*	1	
2	5	Ice alone for 2½ hr. (min. temp. 5·5° C.)	24	,,	,,	,,	2*	,,	1§	1*	4	* Fed recently. § Empty.
3	5	Water 9–10° C. for 4 hr.	24	1§	,,	,,	*Nil*	1*	*Nil*	*Nil*	2	* Fed, digested.
4	7	Ice and water for 3 hr. (min. temp. 2·0° C.)	24	4	10†	,,	,,	*Nil*	,,	3	17	† Some fed.
5	10	Ice and water for 3 hr. (min. temp. 2·0° C.)	24	15†	*Nil*	,,	,,	,,	3*	*Nil*	18	† Ten fed. * All fed.
6	14	Ice and water for 1 hr. (min. temp. 2·0° C.)	24	24*	.	.	.	.	.	.	24	* All fed.
7	16	Ice alone for 2½ hr. (min. temp. 6° C.)	12	10	*Nil*	*Nil*	*Nil*	1	*Nil*	*Nil*	11	
8	16	Water 9–10° C. for 3 hr.	12	*Nil*	,,	,,	,,	*Nil*	,,	,,	*Nil*	Two larvae dropped on 7th day.
Control		Age in days at time of exposure		1	5	7	10	14	.	.	.	
(Separate batches)		Deaths within 7 days (per cent.)		*Nil*	7	20	*Nil*	5	.	.	.	

It is possible that some of the insects used in test No. 1 had taken food, as in captivity *G. palpalis* will sometimes feed on the day of eclosion. The tsetse used in tests 4 and 5 had certainly fed and the survivors a week after exposure had fed again, at least once, so it is possible for these insects to have had a meal and still escape immediate or even delayed death after cooling to 2·0° C. for three hours, and also to feed safely after cooling (*cf.* Potts, 1933, who found that the insects fed, but if they died subsequently contained undigested food and suspected digestive upset as a cause of mortality). It is apparent that cooling to 9–10° C. for three hours has no deleterious effect on the viability of *G. palpalis fuscipes*, up to 16 days old. Such temperatures are probably rare in its natural habitat but are common for several weeks in the year in some places inhabited by *G. morsitans*, which was expected to survive as well as *G. palpalis* and was the species chosen for an experiment on wild flies.

FIELD TESTS.

Tsetse are poor laboratory animals and laboratory findings should be confirmed in the field if possible, before they can be accepted as normal. This was done with samples of non-teneral tsetse flies, principally *G. morsitans*, collected

in the woodland near Magugu, Tanganyika Territory (35° 45′ E.; 4° 0′ S.). Flies were captured between 15.00 and 18.00 hours and were placed in tubes kept in a thermos jar at 10° C. (± 0·5° C.). After collection was complete the tubes were transferred to another flask containing water at the required temperature, which was maintained by the addition of ice water as required. After the appropriate period the tubes were removed and flies released at dusk into a large cage suspended in a room. At dawn all insects which were non-viable (dead or unable to fly) were removed and the survivors then collected separately and killed. This procedure was adopted to approximate to that used in dispersal trials in the field, where flies were released into the cage late in the afternoon and freed at dusk. The treatment was rather more severe than that used in these field trials in that the insects were confined without chance of escape for some hours, a procedure deleterious to tsetse in the daylight hours. On the other hand, flies which were prepared to fly after dusk could escape in the field and would be assumed to survive, although they might die later.

Batches of non-teneral male *G. morsitans* were confined at different temperatures for varying periods. Sixty or more were used except for exposures of 10 min. and 30 min. at 2° C., for which only 30 were available. Except for experiments at 8° C. and 10° C., the initial period of confinement immediately after capture is not included in the recorded exposure time, since it was thought that confinement at 8–10° C. would not harm the insects. At 8° and 10° C. the period quoted is the mean. The process of capturing two samples of about 60 each took about 90 min., and 45 min. is added to the period spent at the designated temperature after capture was complete. Flies were placed in the tubes in strict rotation, which made it possible to divide them into samples containing the same number of flies which had been captured at the beginning and end of the operation.

Results.

The percentage mortalities are given in Table II. The periods and temperatures used are again somewhat miscellaneous owing to the desirability of testing likely field procedures.

Table II.—*Percentage mortality of non-teneral male* G. morsitans *exposed to low temperatures.*

	Exposure time.						
		Hours.					
Temperature	*10 min.*	½.	*1.*	*2.*	*3.*	*4.*	*6.*
10° C.	.	.	.	.	9	.	25
8° C.	.	.	.	.	.	9	16
6° C.	.	.	.	.	.	15	38
4° C.	.	.	.	.	.	48	.
2° C.	42	63	75	80	.	.	.

It will be seen that mortalities increase both with depression of temperature and time of exposure. Even at 10° C. mortalities after several hours are not negligible, as they had appeared to be in field experiments where the insects were free to escape at any time after dusk. There was no relation between hunger stage at the time of exposure and subsequent mortality.

For the most severe treatments used (one and two hours at 2° C.) the mean age of survivors and of casualties has been calculated from the " mean wing fray " (Jackson, 1946). The mean age of the dead was 33 days, of the survivors 18 days. This difference has been tested for significance by constructing a contingency table separating the numbers in each category which fall in the first three classes of wing fray (young flies) and the last three (old flies). The difference is significant at $P = 1$ per cent. The numbers of casualties in the milder treatments were too small for a test to be made on any one of them. Hence the casualties of all treatments at 6°, 8° and 10° C. have been put together and compared with a sample of the survivors made up from each test in the same proportion as the casualties (in order to avoid weighting the result by including too many insects from any one of the three experiments). The mean ages are 26 and 21 days respectively. The difference, tested as before, is not significant (P between 10 per cent. and 5 per cent.).

At the same time as male *G. morsitans* were collected a number of female *G. morsitans* and of male *G. swynnertoni* Aust. were captured and treated in the same manner; numbers of both were much smaller than of male *G. morsitans*. It can only be said that mortality of female *morsitans* was sometimes rather less and sometimes a little more than that of the males, and male *G. swynnertoni* were consistently more vulnerable. In all tests with male *G. swynnertoni* a total of 23 survivors was available for comparison with 41 casualties (some others were destroyed before wings could be taken). The mean age of survivors was 18 days, of casualties 23 days. The sample of survivors is too small for a proper test of significance, since the total falling among the " old " flies is only 3, too small for a χ-square test. If the division between young and old is made between classes 2 and 3 of the wing-fray classification a test is possible, but the resulting value of P is not significant.

Discussion.

There is a tendency for old wild *G. morsitans* and *G. swynnertoni* to die more easily from cold than the young flies. More remarkable is the fact that deaths occur at temperatures frequently met at certain seasons in natural fly habitats. That it is the older, breeding section of the population which succumbs suggests that cold may be an important factor in limiting tsetse distribution by directly killing off flies as well as by slowing down breeding and development. From the point of view of the use of chilling as a means of handling flies for experiments, the results are discouraging if it is desired to study the behaviour of the insects after release. In practice we have cooled flies to between 8° and 10° C. and the number found dead in the cage the morning after release has been about 5 per cent., which could be put down to rough handling by the catchers. A field experiment has been made in which captures of insects cooled to 8–10° C. and to 2–3° C. were compared to recaptures of flies marked, and released as captured, in an earlier year at the same season in the same isolated piece of woodland. (For these last figures I am indebted to the late Dr. C. H. N. Jackson). In contrast with our original experiment at Urambo, recaptures of both sets of chilled flies were relatively depressed in the first four days after release. There is a gap in the data after the first week but in the fourth week recaptures of flies chilled to 8–10° C. were only half, and of those cooled to 2–3° C. only one-sixth as numerous as the corresponding

recaptures of Jackson's unchilled flies, after due allowance for pre-release deaths. The numbers were too small for a satisfactory test of significance, but the use of chilling as a method of transporting tsetse cannot be recommended for experiments which depend on normal survival and behaviour of the flies after release. Tests have not been made for temperatures over 10° C., since the insects take a long time to become immobile and revive rapidly when the tubes are removed from the flask. This makes it difficult to handle large numbers and defeats the object of the method. When only a few flies are required, one or two per tube, cooling to 15° C. might be practicable and seems unlikely to harm the insects.

These results confirm and explain the initial findings from dispersal experiments in the field—better survival of young flies and the falling-off in recaptures after the first four days. The findings may also reconcile conflicting reports on the effect of cold on tsetse (e.g. Macfie 1912 ; Potts 1933 ; Geigy 1946 ; Vanderplank, *unpublished*), since different investigators may have used specimens of different ages.

Summary.

It has been shown with both laboratory-emerged *G. palpalis* and wild-caught *G. morsitans* and *G. swynnertoni* that old flies of both sexes are more susceptible to cold than young ones. There was no evidence that deaths are due to digestive failure. In only one wild-caught sample (of *G. morsitans*) was this difference statistically significant but the trend is constant. Mortality is appreciable even at temperatures met naturally in tsetse habitats, and it seems likely that this factor acts directly in limiting the distribution of tsetse flies.

Acknowledgments.

Grateful acknowledgment is due to Dr. F. L. Vanderplank and to the late Dr. C. H. N. Jackson for permission to quote and use their unpublished results. The work was financed from Colonial Development and Welfare Scheme funds at the disposal of the Colonial Pesticides Research Committee.

References.

Buxton, P. A., 1955, *The Natural History of Tsetse Flies*. London.

Geigy, R., 1946, Beobachtungen an einer Zucht von *Glossina palpalis*. *Verh. schweiz. naturf. Ges.* **1946** : 155–158. (*Quoted in* Buxton, 1955).

Jackson, C. H. N., 1933, Causes and implications of hunger in tsetse flies. *Bull. ent. Res.* **24** : 443–487.

——, 1941, The economy of a tsetse population. *Ibid.* **32** : 53–5.

——, 1946, An artificially isolated generation of tsetse flies. *Ibid.* **37** : 291–299.

——, 1952, (*Quoting Webb, C. J.*) in *Rep. E. Afr. Tsetse Trypanosomiasis Res. Reclam. Organisation*, **1951**. Nairobi.

Macfie, J. W. S., 1912, Experiments and observations upon *G. palpalis*. *Bull. ent. Res.* **3** : 61–72. (Not seen in original, *quoted by Vanderplank, below*).

Potts, W. H., 1933, Observations on *G. morsitans* in East Africa. *Ibid.* **24** : 293–300.

Vanderplank, F. L., *Unpublished Thesis*, Univ. Bristol.

THE LARVAL MORPHOLOGY OF AGROMYZIDAE (DIPTERA).

By Pamela Allen.

(*Dept. of Zoology, Glasgow University.*)

Introduction.

Initial investigation of the early stages of Agromyzid flies was made by the late Professor J. C. H. de Meijere. He described the general larval features of the family and also larvae of many species (1925–50). Some of his material was obtained from Professor E. M. Hering, who, since de Meijere's death in 1947, has continued the larval descriptions on the same lines.

The only key to Agromyzid larvae so far published is that of K. E. Frick (1952), which separates only the genera according to variations in the structure of the mandibles and cephalopharyngeal apparatus. Although, like all Cyclorrhaphan larvae, there is an apparent uniformity of structure in the family, a detailed examination reveals many variable characters which it should be possible to use in constructing a key to species level. Such a key would be of value in the study of relationship between species, and even, perhaps, of their validity. It would have undoubted practical value, too, for there are a number of species in which the imagines are so similar as to be difficult to separate, and it could also be used on the many occasions when heavy parasitism prevents the rearing of adults.

The following paper is a critical re-examination of the larval morphology as a preliminary to the construction of a key.

Methods.

Investigation of the larval morphology may be made using third instar larvae, either living or fixed and stained. It is best to use third instar larvae, which are biggest and show cuticular structures most clearly. When the larva is a stem miner, it can usually be examined and replaced in the stem without affecting its development, provided it is carefully handled. Leaf miners cannot usually be removed from the mine without causing death, so that, if adults are to be reared from the material, it is not desirable to examine the larvae. However, a permanent record of external larval structure, with the exception of the head segment, is to be found in the puparium, which is, of course, the stiffened cuticle of the third instar larva, and is available for examination after emergence of either adult Agromyzid or parasite.

The puparium is stiffened by the deposition on its inner surface of the calcospherites which are formed in the larval fat body (Keilin, 1921,). These can be dissolved by dilute hydrochloric acid and, after taking out the prepupal and pupal exuviae, the puparium, now quite soft, can be cut open and spread flat on a microscope slide for examination. Concentrated acid should not be used, as the violent effervescence produced causes shrivelling of the cuticle, and wrinkles appear which obscure all other features. The mouthparts can be reclaimed from within the anterior part, and the puparium is then more easily examined than the larva itself.

Proc. R. Ent. Soc. Lond. (A) 32. pts. 4–6. (June, 1957).

For structure of the head segment, or for the shape of the spiracles in the expanded condition, it is necessary to study the larva before pupation. Many larval features can be seen without special treatment, but, if staining is necessary, a satisfactory technique is described by Hering (1954), using Basic Fuchsin and Orange G.

Structure of the Puparium.

(a) *Before Treatment with Acid.*

Puparia vary in shape from elongated, almost cylindrical, to ovoid. As a rule, the stem mining species have the most elongate form, and those leaf miners which pupate outside the mine the most rounded (fig. 1). Colour, too, has a wide range, from almost white, through shades of brown, to black, being usually uniform, but sometimes with a dorsal and ventral stripe of a darker colour.

There are eleven segments present: three thoracic and eight abdominal. The larval head region is withdrawn into the thorax, and the prothoracic segment is contracted at this point and forms the first segment of the puparium. The boundaries between the segments may be clearly marked by constrictions, or may be almost indistinguishable, and the surface texture varies from smooth and shiny to relatively matt, with ridges.

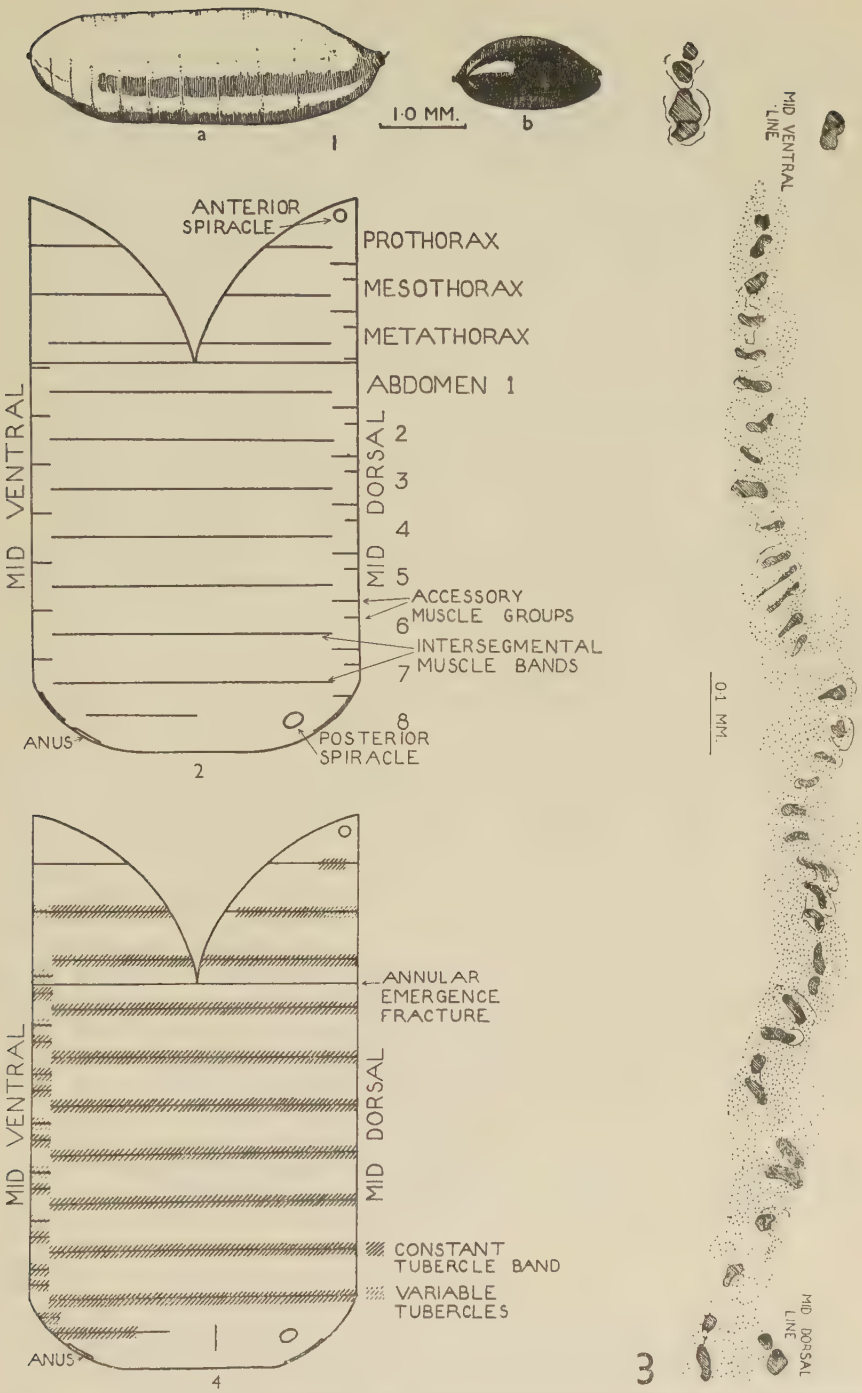
The spiracles are found on the prothorax and the eighth abdominal segment and, although contracted, display the larval features. In species which pupate within their mines, the spiracles may show a characteristic elongation associated with their penetration of the plant epidermis. At this stage it is usually not possible to distinguish more than their general shape, but after acid treatment they can be more minutely examined.

The anus, on the eighth abdominal segment, may be difficult to see, but in some species a more or less conical projection is present on either side of it, and these projections, or " anal lobes ", are readily visible.

Emergence of the imago takes place by means of two or three breaks in the wall of the puparium at its anterior end—a circular split, running completely round the puparium at right angles to its long axis, and a lateral split dividing the anterior part into a dorsal and a ventral portion, of which the former may be divided again in the mid-dorsal line. These parts, broken off at emergence, often remain with the rest of the puparium, held with it by the pupal and prepupal exuviae.

(b) *After Treatment with Acid.*

Puparia mounted on microscope slides can be examined in more detail. The segment boundaries are discernible as lines of cuticular thickening which have served as points of attachment for muscles. These " muscle scars " are present as a more or less undulating line, running either completely round each segment boundary, or having a dorsal and a ventral break. One, or two, supplementary groups of muscle scars may be present in the mid-ventral or mid-dorsal line, lying, not on the boundary, but in the segment itself. Figure 2 shows a simple method of representing diagrammatically the pattern formed by the muscle scars. It does not indicate the undulations which they make, nor their individual shape and number, but will serve as a basis for more complex diagrams.



FIGS. 1–4.—(1) Puparia of (*a*) *Melanagromyza angelicae* (Frost), a stem miner ; (b) *Phytomyza anthrisci* Hendel, a leaf miner. (2) Muscle scar band pattern of *Ophiomyia maura* (Meigen). (3) Post-third abdominal tubercle band of *Napomyza lateralis* (Fallén). (4) Tubercle band pattern of *Phytomyza anthrisci* Hendel.

The breaks for emergence of the imago take place along definite lines of weakness. These can be seen quite clearly, even in the parasitised puparium. The annular split may occur in the centre of the first abdominal segment or of the metathorax, or may be oblique, lying dorsally in the abdomen and ventrally in the thorax. The lateral split always divides the thorax so that the spiracles remain in the upper half and the cephalopharyngeal apparatus in the lower.

Bands of cuticular processes (" Warzengürtel " of de Meijere) occur between many of the segments. They are composed of many little warts or tubercles, and lie in the region of the muscle scars, although the latter are on the inside of the cuticle and the tubercles on the outside (fig. 3). Often the area directly overlying the individual muscle scars is left clear. There may be a definite arrangement of the tubercles in rows, often of two distinct sizes of process, but in many species they are scattered irregularly in an intersegmental band, lying partly on the posterior portion of one segment, and partly on the anterior portion of the segment behind. The tubercle bands are usually best developed laterally, and it is to this area that most of de Meijere's descriptions apply. The bands are not present in all regions, nor are they necessarily continuous around the intersegmental boundary. Some variation does occur within species, especially where there are small ventral groups associated with supplementary muscle scars, but a specific pattern appears, which, like the muscle scars, can be represented diagrammatically, and in the same way. However, owing to the slight individual variations, it is desirable that description should be based on examination of more than one specimen.

Figure 4 expresses the pattern of tubercle bands in relation to the muscle scars, and also shows the segment in which the annular break occurs. It must be stressed that only the pattern is represented, and not the relative proportions of band width to segment width, etc. This is best expressed by giving the measurements of a stated band and a stated segment, taking the measurement at the side of the body. The pattern diagram can also be supplemented by an accurate scale drawing of part of a band, showing tubercle size and distribution, and muscle scar size, shape and undulation. It is convenient to name the tubercle bands according to the segment immediately in front of them—thus, post-prothoracic band, post-seventh abdominal band, etc. There may be a small group of tubercles below or around the anus—the sub-anal group.

Sense papillae can often be seen on the puparium. On the prothorax the contraction consequent on the withdrawal of the head makes their situation difficult to assess, but on the other segments they can usually be found in a ring around the segment, half way along. Their number is somewhat variable, but may have a certain significance. Sense papillae are found also on the eighth, or last, abdominal segment. Here they often form a definite arrangement, but are not always easy to see because of the difficulty of making this segment lie flat on the microscope slide.

The Mouthparts.

Mouthparts can be recovered from the first and second exuviae present in old mines, but, whereas those of second and third instar are similar, the first instar mouthparts are of a simple form. Figure 5 shows the mouthparts of the three instars of *Phytomyza obscurella* Fallén. Mouthparts taken from the puparium are, of course, third instar.

The mouthparts consist of mandibles and cephalopharyngeal apparatus. Frick (1952) describes their usual structure and homologies; figure 6 illustrates the terms used by him. I would like to make the following suggestions and additions: it will eliminate confusion if the dorsal and ventral arms of the dorsal process are referred to as upper and lower arms. Where the upper arm bends sharply the angle so formed can be called the dorsal angle, and its position may be important. The dorsal process is paired, but the ventral process is a single structure, which is evenly sclerotised in some species, but in others a short dorsal or upper branch is found on each side, or a pair of foramina (fig. 5).

Structure of the Larva.

In the larva the spiracles are in an expanded condition and, although it is usually possible to see details in an acid-treated puparium, they are more easily investigated in the larva. In some species the spiracles always terminate in three orifices or " bulbs ", but the majority have a large number of bulbs; for such species the number is not constant.

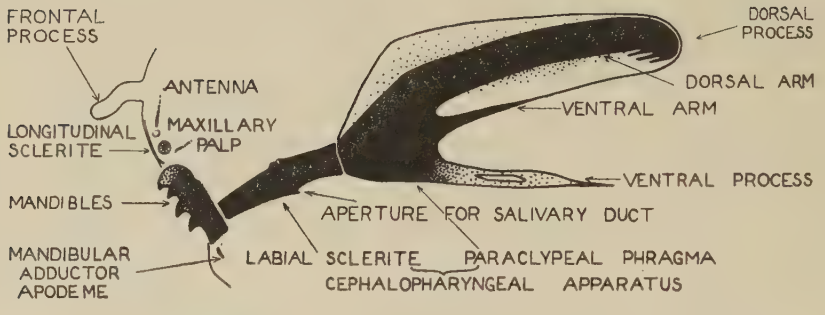
One feature which cannot be examined in the puparium is the facial mask. This is a term applied to the structures on the ventral surface of the head surrounding the mouth, and comprises bar-like sclerotisations of dark colour and characteristic shape, sense papillae, antennae and maxillary palps, and a finger-like process sometimes present, the " Stirnfortsatz " or frontal process. Figure 7 is a diagram of a generalised facial mask; the following terms may be used to describe it:

Areola—a hemispherical protuberance, bearing one or more sense papillae.
Principal areola—the areola bearing the antenna and maxillary palp.
Anterior areola—that which lies in front of the principal areola.
Intermediate areolae—three on each side of the mandibles, behind the principal areola.
Antero-lateral sclerites—sclerotisation around the outer edges of the principal areolae. These may be the mandibular abductor apodemes mentioned by Frick (1952).
Lateral sclerites—wing-like appendages to the base of the mandibles.
Sense papillae—*A*, on the anterior areola.
P_1, on the principal areola, in front of the antenna.
P_2, between the antenna and maxillary palp, on the inner side.
P_3, between antenna and palp, on the outer side.
P_4, behind the maxillary palp.
I_1, I_2, I_3, on the intermediate areolae.
L, on the lateral sclerite, or level with the base of the mandibles.
H, on the posterior border of the head segment.

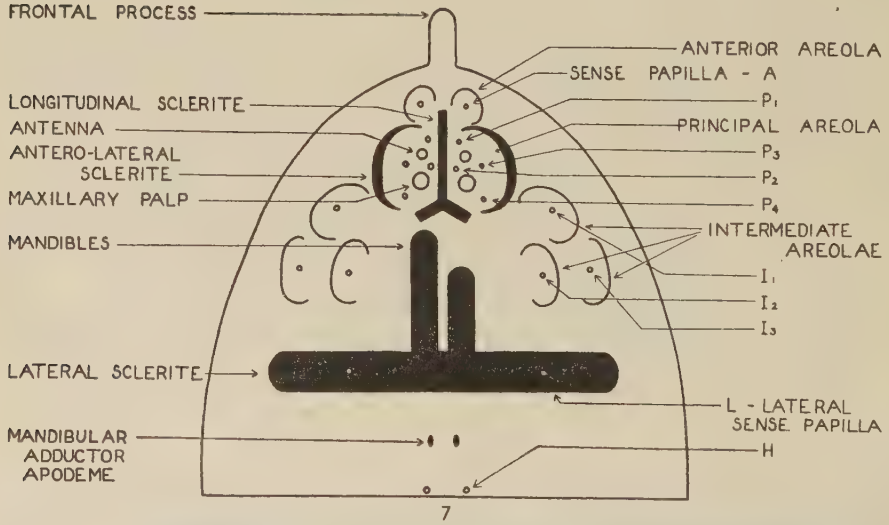
Discussion.

Although it is desirable that descriptions should be as full as possible, not all the characters described will be of value in constructing a key, except for confirmation. Suitable characters will be those which admit least doubt, giving the sharply defined positive or negative dichotomy which is especially desirable if the key is to be of use to a non-specialist.

5



6



7

FIGS. 5–7.—(5) Mouthparts of the three larval instars of *Phytomyza obscurella* Fallén. (6) Diagrammatic representation of mouthparts, named according to the terminology of Frick (1952). (7) Generalised facial mask.

Frick has separated the North American genera by differences in the structure of the mouthparts. Generic differences will probably be found also in the muscle scar band pattern and in the position of emergence fractures on the puparium. Specific differences will lie in variations in shape, colour, texture and degree of indentation of the puparium, and in the tubercle band patterns. In a few species the shape of the spiracles may be important, especially where any marked elongation occurs, or where the number of bulbs is constant, but if the number is not constant this will be an unsatisfactory character to use. The shape of the mouthparts is rarely distinctive enough to differentiate species, at least in the genus *Phytomyza*. Sense papillae, those of the facial mask and the last segment, may be valuable, but are not always easy to see. Tubercle shape and muscle scar shape may be important in a few species.

It is unfortunate that muscle scar band and tubercle band patterns have not been fully described in the past, nor have the emergence fractures of the puparium, but it is hoped that future descriptions or redescriptions of larval forms will remedy this. If other workers on the family have larvae or puparia which they do not wish to describe themselves, I would be pleased to receive any such material.

The following key has been constructed to separate certain species feeding on Umbelliferous plants in this country, and is given here as an example of a key using only larval characters.

Key to Some Agromyzidae from Umbelliferae.

1 Upper and lower arms of dorsal process of paraclypeal phragma both well developed. Suture present between paraclypeal phragma and labial sclerites. Anterolateral sclerites present 2

— Lower arm reduced or absent. Suture incomplete or absent. Anterolateral sclerites absent 3

2 Annular emergence fracture confined to first abdominal segment **Ophiomyia maura** (Meigen)

— Annular fracture occurs ventrally in metathorax, and dorsally in first abdominal segment . . . . . **Melanagromyza** spp.

3 Lower arm of dorsal process of paraclypeal phragma absent; ventral process without foramina. Annular fracture in metathorax **Napomyza lateralis** (Fallén)

— Lower arm much reduced, but usually present; ventral process with foramina. Annular fracture in first abdominal segment **Phytomyza** spp. 4

4 Puparium smooth and shiny; intersegmental indentations scarcely visible. With or without frontal process 5

— Puparium deeply indented. Without frontal process 9

5 Abdominal tubercle bands broken in the mid-dorsal line **P. melana** Hendel

— Some, at least, not broken 6

6 Successive posterior abdominal tubercle bands fused ventrally **P. obscurella** Fallén

— Little or no ventral fusion 7

7 Post-prothoracic tubercle band absent . . . . **P. tordylii** Hendel

— Post-prothoracic tubercle band present dorsally 8

8 Sub-anal tubercle group present **P. anthrisci** Hendel and **P. conopodii** Hering

— Sub-anal tubercle group small or absent . . . . . **P. silai** Hering
9 Puparium rough and ridged 10
— Puparium smooth and shiny, though with deep indentations **P. angelicastri** Hering
10 Anal lobes present. Post-prothoracic tubercle band present dorsally ; sub-anal group absent . . . . . **P. angelicae** Kaltenbach
— Anal lobes absent. Post-prothoracic tubercle band absent ; sub-anal group present . . . . . **P. spondylii** Robineau-Desvoidy

Summary

The features of Agromyzid larvae and puparia are described, and a method is proposed for illustrating the pattern formed by the muscle scars and tubercle bands. It is suggested that future descriptions should include these patterns, and that they will be valuable in the construction of keys. Attention is also drawn to the probable importance of the distribution of sense papillae on the head and the last segment and of the position of emergence fractures on the puparium.

Acknowledgments.

This work was begun at the Imperial College Field Station, Sunninghill, Berks., where I received advice from Professor J. W. Munro, Professor O. W. Richards and Dr. W. F. Jepson, and continued at the Queen's University of Belfast, which, with the Ministry of Education (N.I.), financed my research at this period. The work is now being continued at the University of Glasgow. I am indebted to all these institutions for the facilities which they have provided.

References.

Frick, K. E., 1952, A generic revision of the family Agromyzidae (Diptera) with a catalogue of New World species. *Univ. Calif. Publ. Ent.* **8** : 339–452.

Hendel, F., 1931–36, Agromyzidae *in* Lindner, *Flieg. Pal. Reg.* **59**, 570 pp.

Hering, E. M., 1954, Die Larven der Agromyziden (Diptera). I. *Tijdschr. Ent.* **97** : 115–136.

——, 1956, Die Larven der Agromyziden (Diptera). II. *Ibid.* **98** : 257–281.

Keilin, D., 1921, On the calcium carbonate and the calcospherites in the Malpighian tubules and the fat-body of Dipterous larvae and the ecdysial elimination of these products of excretion. *Quart. J. micr. Sci.* (2) **65** : 611–625.

Meijere, J. C. H. de, 1925–26, Die Larven der Agromyzinen. *Tijdschr. Ent.* **68** : 195–293 ; **69** : 227–317.

——, 1928–50, Ditto. Nachtrag (1)–(9). *Ibid.* **71–92**. (1) 1928, **71** : 145–178 ; (2) 1934, **77** : 244–290 ; (3) 1937, **80** : 167–243 ; (4) 1938, **81** : 61–116 ; (5) 1940, **83** : 160–188 ; (6) 1941, **84** : 13–30 ; (7) 1943, **86** : 61–76 ; (8) 1946, **87** : 65–74 ; (9) 1950, **92** : 15–33.

——, 1955, Die Larven der Agromyziden (Diptera). General-Register. *Ibid.* **98** : 1–27.

ON THE ROLE OF THE TRACHEAL SYSTEM IN THE POST-EMBRYONIC GROWTH OF *LOCUSTA MIGRATORIA* L.

By Kenneth Upex Clarke.

(Zoology Department, University of Nottingham).

I. Introduction.

Previous studies on the growth of insects have shown that the weight increases and the linear dimensions of the instar remain unchanged during a stadium, while at an ecdysis the weight decreases slightly and the linear dimensions increase (Eidmann, 1924; Teissier, 1931). This being so Teissier (1931) deduced that the density of an insect shows a cyclical change, increasing during a stadium and decreasing at an ecdysis. The increase in size of the tracheal system occurs only at ecdysis (Deegener, 1904; Tiegs, 1922; Kuhn and Piepho, 1938; and Keister, 1948). The correlation of these changes in the growing insect suggests that, while the amount of tissue and density increase during a stadium, the tracheal system remains constant in size. At an ecdysis the amount of tissue remains approximately the same, the density decreases and the size of the respiratory system increases. This is an unusual relationship, and it was therefore thought worth while to try to verify the theoretical conclusion of Teissier, and to see if the simple relationship outlined above was true in the case of the locust.

II. Material and Methods.

The insects studied were females of the third, fourth, fifth and growing phase of the adult instar of *Locusta migratoria migratorioides* (R. and F.), stocks of which were obtained from the Anti-Locust Research Centre, London. The animals were kept in an insectarium the temperature of which was thermostatically controlled at 28° C. and which had a Relative Humidity of 75 ± 5 per cent. The photoperiod was 12 hours light alternating with 12 hours dark, the light intensity being 17-foot candles on the floor of the cages. These lights caused a daily rise of 2° C. in the temperature, which followed a regular daily cycle with a maximum of 30° C. between 12.00 and 22.00 hours, and a minimum of 28° C. between 00.20 and 09.30 hours. The stock population was kept at densities greater than 100 individuals per cage of 18 inch cube, and the experimental animals at densities greater than 4 per cage (1 pound Kilner Jar, 500 ccs.). None of the locusts showed any evidence of phase change under these conditions. Abundant fresh food in the form of grass was available at all times.

The following technique was used to obtain a series of samples of locusts of different ages spanning each stadium. A population for sampling was prepared by taking from stock all locusts younger than the instar it was proposed to study. This population was made up of a large number of individuals of very diverse ages, so that each day some might be expected to moult to the required instar. The population was examined at frequent intervals, and at each observation those locusts that had moulted to the required instar were

removed. Each batch was kept separately in a cage and formed a single sample. The intervals between observations were approximately 12 hours; in each case the exact interval was recorded. The first sample was used to determine the duration of the stadium and, when half the locusts of this sample had moulted to the succeeding instar, the other samples were used for the experiment. At this time the second sample containing the oldest individuals might be expected to be within 12 hours of their final moult, while the most recently-taken sample, usually the eleventh or twelfth, would contain locusts that had moulted to the required instar within the last 12 hours. This method gave a series of samples of different known ages that could be used at one time for the experimental determination of their characteristics.

The duration of each stadium was taken as the period in hours that elapsed between the midpoint of the two observations straddling the entry of the locusts into the stadium, and the midpoint of those which straddled the exit of all members of the sample from the instar. The age of each sample was taken as the difference in hours between the midpoint of the two observations which straddled the entry of the sample into the instar and the time at which the sample was used for the experiment. Times of observations were exactly recorded; in no case did the interval between observations at an initial ecdysis exceed 12 hours (minimum time 2 hours), or that between those straddling a final ecdysis exceed 16 hours (minimum 6 hours).

The measurements made on each individual were—weight in milligrams, and volumes of the animal and of the tracheal system in $mm.^3$

The method of measuring the volume of the tracheal system was adapted from an injection technique described by Wigglesworth (1950). The principle was to weigh the locust and then fill the tracheal system with fluid of known specific gravity and re-weigh it; from the difference in weight the volume of fluid in the tracheal system was calculated. Wigglesworth gives a full description of the apparatus used and of the method of injection, so that it is only necessary to mention the procedures which adapted the technique to the present purpose.

Each individual locust was weighed, placed in the gauze container in the apparatus and exposed, first to a vacuum of 550 mm. of mercury for two minutes, and then to an atmosphere of hydrogen for one minute. This was repeated, and the locust then exposed to the vacuum for three minutes, after which it was pushed below the surface of the fluid and air at atmospheric pressure admitted to the container. The insect was kept in this position for 15–20 seconds before being removed from the container. It was then dried by touching its surface with filter paper, particular care being taken to dry beneath the wing pads and the pronotum, between the mouthparts and around the bases of the legs. Drying was completed by blowing dry air on the animal, thus causing any remaining fluid to evaporate. The locust was then re-weighed, the difference between the two weighings giving the weight of fluid in the tracheal system.

The volume was measured by immersing the locust in fluid in a measuring cylinder and noting the displacement that occurred. The locust was then removed and dissected under a binocular dissecting microscope to see if the fluid had completely filled the tracheal system. The fluid used was petroleum ether containing cobalt naphthenate and having a specific gravity of 0·790 at

20° C., which could be easily seen in the tracheae and tracheoles. Those of the brain, gut, wing muscles, as well as the air sacs and lateral trachea, were examined. If these were full of fluid and there was an absence of air bubbles from all parts of the system, the locust was judged to have been successfully injected and the volume of fluid in the trachea to be equal to the volume of the tracheal system.

The main sources of error in this technique were (1) loss of weight, due either to defaecation between the two weighings or to loss of water whilst in the vacuum, and (2) gain in weight due to the tar-like cobalt naphthenate adhering to the exoskeleton. In the first event, detectable by finding the faecal pellet in the gauze container, the animal was rejected as being useless because the weight of the pellet when it left the locust could not be determined. Experiments showed that loss of weight due to the seven minutes exposure under the vacuum averaged 0·4 per cent. of the initial weight, while gain of weight due to cobalt naphthenate adhering to the exoskeleton averaged 0·7 per cent. of the initial weight. These figures suggested that the error introduced by the technique amounted to approximately + 0·3 per cent. of the animal's weight and, in comparison with the changes measured, was small enough to be ignored.

III. Results.

The actual values obtained for different individuals for weight, volume of the animal and tracheal volume are illustrated in figure 1, which is based on one series of observations of the fourth instar. Before considering the changes shown, there are two further important factors to be calculated from the individual measurements, namely the volume and density of the tissues of the locust.

The volume of the insect could have two meanings. In the first place there was the volume of space occupied by the locust and its enclosed systems, which was measured by immersing it in fluid in a measuring cylinder, and which will be referred to as the immersion volume. In the technique used the tracheal system was already full of fluid, so that there was no error in this volume measurement due to the fluid entering into it. Secondly, a considerable part of the immersion volume (8–40 per cent.) was occupied, not by the tissues of the body, but by air in the tracheal system. The volume of the tissues was calculated by subtracting the volume of the tracheal system from the immersion volume. This was called the tissue volume and was calculated for each individual.

Just as the volume of the locust could be expressed in two ways, so could its densities, these being :

$$\frac{\text{weight}}{\text{immersion volume}} = \text{immersion density} \quad . \quad . \quad . \quad (1)$$

$$\frac{\text{weight}}{\text{tissue volume}} = \text{tissue density} \quad . \quad . \quad . \quad (2)$$

Both values were calculated for each individual.

When the measured values for weight, immersion volume and tracheal volume, as well as the calculated value for tissue volume, were plotted against

time for any instar measured, it was found that the general trend could be adequately expressed by a straight line (fig. 1). The trend for the tracheal system is not so well represented by a straight line as are the other characteristics, since the decrease in volume was more rapid at the commencement of the stadium and there was a slight increase in volume just before the ecdysis. Nevertheless, it was doubtful if fitting a curve of greater complexity would

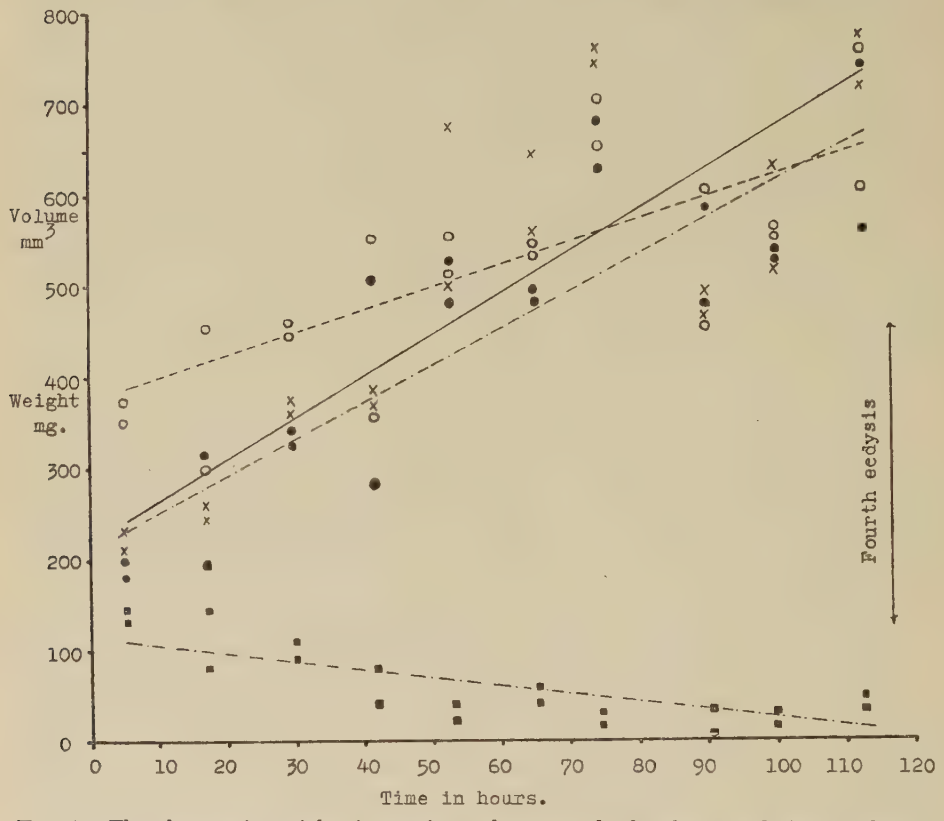


Fig. 1.—The changes in weight, immersion volume, tracheal volume and tissue volume during the fourth stadium. ×, *observed weight (mg.)*; ○, *observed immersion volume (mm.³)*; ■, *observed tracheal volume (mm.³)*; ●, *calculated tissue volume (mm.³)*. ————, *Regression of weight/time*; – – – –, *regression of immersion volume/time*; —·—·—·, *regression of tracheal volume/time*; – –·– –·– –, *regression of tissue volume/time.*

contribute anything to the analysis of this change, and a straight line representation of the general trend was therefore accepted.

Accordingly parameters were calculated for the formula

$$y = a + b\,(x - x') \quad . \quad . \quad . \quad . \quad . \quad (3)$$

where y is the value of the quality, x is the time, and x' is the mid-point of the stadium in time, and a and b are constants which were calculated by the method of least squares and are given in Table I together with their standard

Table I.—Values of formula $y = a + b(x-x')$ *for weight, immersion volume, tissue volume and tracheal volume of stadia 3, 4 and 5 and the growing phase of the Adult Stadium A.*

Stadium.	Size of sample.	Value of x^1 (hours).		a and its standard error.	b and its standard error.
3	36	52·9	Weight in mg.	183·60± 5·47	1·66±0·12
			Immersion volume mm.^{3}	185·80± 3·71	1·29±0·13
			Tissue volume mm.^{3}	169·35± 4·06	1·68±0·15
			Tracheal volume mm.^{3}	16·48± 1·26	−0·39±0·01
4 (1)	26	70·5	Weight in mg.	529·40±18·41	3·75±0·54
			Immersion volume mm.^{3}	536·50±13·82	2·67±0·40
			Tissue volume mm.^{3}	484·70±23·10	2·83±0·67
			Tracheal volume mm^3	49·29± 3·56	−1·12±0·10
4 (2)	21	61·02	Weight in mg.	498·80±23·00	4·16±0·67
			Immersion volume mm.^{3}	512·80±17·29	2·46±0·50
			Tissue volume mm.^{3}	456·80±18·61	3·48±0·54
			Tracheal volume mm.^{3}	51·21± 4·87	−0·84±0·14
5 (1)	45	85·23	Weight in mg.	1073·00±12·84	5·32±0·27
			Immersion volume mm.^{3}	1143.00±69·71	2·36±1·44
			Tissue volume mm.^{3}	980·60±24·96	5·25±0·51
			Tracheal volume mm.^{3}	156·80±11·58	−2·80±0·24
5 (2)	24	90·2	Weight in mg.	1238·00±33·30	8·81±0·73
			Immersion volume mm.^{3}	1519.00±42·04	6·25±0·92
			Tissue volume mm.^{3}	1234.00±40·73	9·26±0·90
			Tracheal volume mm.^{3}	248·80±42·85	−3·02±0·94
A	35	144·14	Weight in mg.	1744.00±49·80	2·20±0·31
			Immersion volume mm.^{3}	2202·80±44·97	0·98±0·28
			Tissue volume mm.^{3}	1858·90±43·11	1·85±0·27
			Tracheal volume mm.^{3}	343·90±19·59	−0·77±0·12

errors. The probability that the observed values for b could have been obtained by chance from a population in which b was zero was also calculated. In all cases this probability was less than 0·01 and usually less than 0·001, indicating that the value for b was highly significant and was the best value that could be obtained for a straight line formula (Mather, 1943).

The unexpected decrease in the volume of the tracheal system during a stadium to about 10 per cent. (see fig. 1) required further consideration. The actual measurement obtained by the technique used was the amount of fluid that could be forced into the tracheal system at different times in the stadium. This amount decreased as the stadium progressed. Dissection of the injected locusts under the microscope showed that in the older specimens the air sacs were less dilated than in the younger ones. They contained very little fluid, although the trachea leading to them and the tracheoles arising from them were filled. There was no air in these air sacs so that they must have emptied when the animal was exposed to the vacuum and they would have filled with fluid had they been able to do so. The decrease in volume of the tracheal system was due to these air sacs being less expanded in the latter than in the earlier parts of the stadium and not due to any shrinkage of the system.

IV. Discussion.

As stated in the introduction, Teissier (1931) deduced that there was a cyclical change in the density of insects which increases during a stadium and

decreases during ecdysis. It is convenient to start the discussion from this point.

When the immersion density was plotted against time it could be seen that the points formed a curve approximating to that calculated by Teissier. This is illustrated in figure 2*B* for the fourth stadium and ecdysis. The mean value

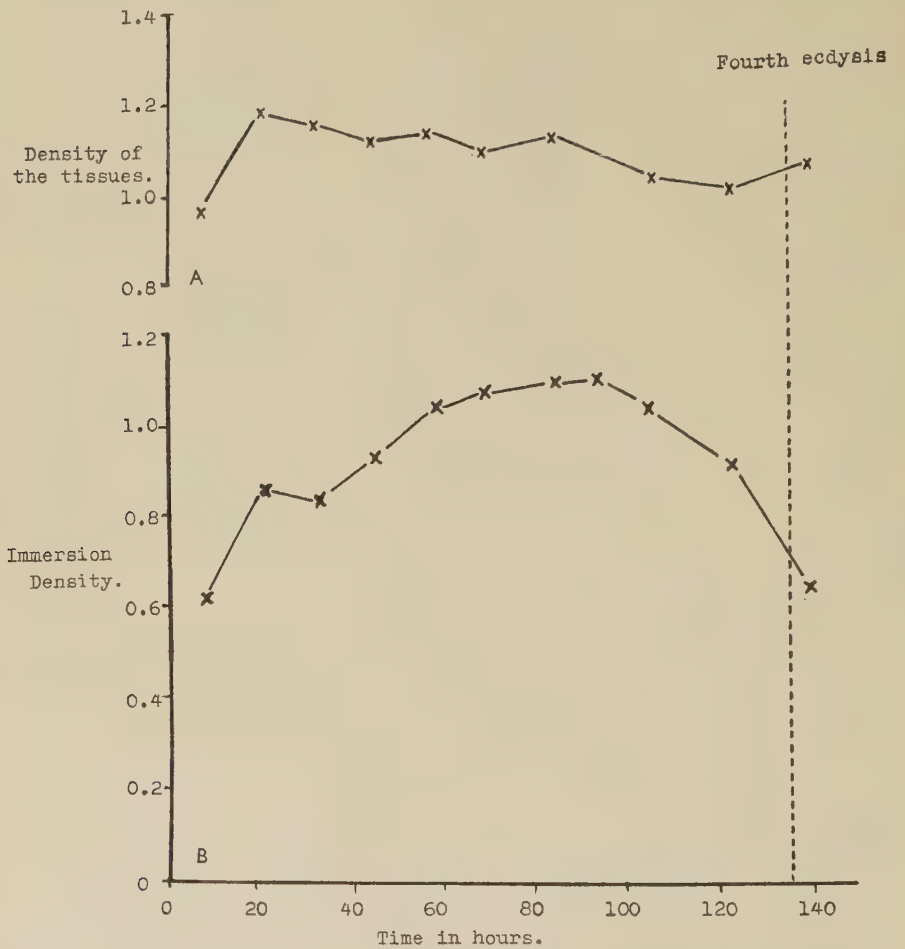


Fig. 2.—(*A*) Changes in tissue density during the fourth stadium and fourth ecdysis. (*B*) Changes in immersion density during the fourth stadium and fourth ecdysis

for immersion density at the commencement of the stadium was 0·612, and this rose to 1·082 at the end of the stadium and dropped to 0·631 at the commencement of the fifth stadium. The maximum density observed was not so great as that calculated by Teissier because, in the locust, there was an increase of immersion volume during the stadium, a factor Teissier did not take into account. The tissue density, based on the same data as the immersion density, did not, when plotted graphically, show any sign of cyclical change (fig. 2*A*).

The values for tissue density were found to be similar for all locusts examined, no matter at what stage in the stadium ; it was 1·064 ± 0·189 for 201 observations. It follows from this that tissue volume varied directly with tissue weight and was not subject to any cyclical changes. This was an important point in the calculation of the changes that took place at an ecdysis.

It did not prove practical to measure changes in weight and volume that took place whilst an ecdysis was in progress. These had to be deduced by comparing locusts measured immediately before and immediately after an ecdysis. Because the samples of known age available were small and variation in weight and volume found within a sample was large, individuals from before and after an ecdysis were paired for comparison, having regard to the following considerations. Reasons have been given for supposing that tissue volume and density were unchanged by an ecdysis, while changes in weight, immersion volume and linear size did occur. Locusts from the end of one stadium were therefore paired with those from the beginning of the next, the pair being chosen so that their tissue volumes and densities were as nearly identical as possible. The differences then found in the other factors were taken to represent the changes they underwent at an ecdysis. Four pairs of individuals were compared for each ecdysis ; the mean of the differences found is given in Table II, together with the mean of the differences found between these same samples compared at the beginning and end of each stadium.

TABLE II.—*Changes in immersion volume, tissue volume and tracheal volume during a stadium and at an ecdysis.*

Stage.	Immersion volume ($mm.^3$).	Tissue volume ($mm.^3$).	Tracheal volume ($mm.^3$).
3rd stadium .	+133·4	+168·0	−38·0
3rd ecdysis .	+106·6	+1·7	+120·2
4th stadium (1) .	+225·0	+336·8	−116·7
4th stadium (2) .	+315·0	+414·3	−98·3
4th ecdysis .	+370·8	+2·4	+371·1
5th stadium (1) .	+352·0	+624·5	−337·4
5th stadium (2) .	+845·2	+1207·0	−362·9
5th ecdysis .	+441·6	+30·4	+442·2
Adult . .	+633·0	+920·5	−288·0

This Table shows quite clearly that the tissue volume increased greatly during a stadium, that the immersion volume increased during a stadium and at an ecdysis by approximately equal amounts, and that the tracheal volume decreased during a stadium and increased at an ecdysis. It is important to note that the increases of immersion volume and of tracheal volume at an ecdysis are nearly equal in amount ; both values were measured independently of each other.

The relationships between the changes in size of the factors measured throughout the cycle of instar and ecdysis may now be considered.

The relationship between tissue weight, tissue volume and tissue density showed no cyclical change at all. Tissue volume and tissue weight varied together, so that the tissue density remained approximately constant. The variation about the mean for tissue density was due to two factors, (1) variation

to be expected between individuals in a population, and (2) that due to the measured weight not being exactly equal to the tissue weight. The measured weight included the tissues and food within the gut ; the amount of food varied from time to time. It is probable that changes in tissue density were very small and that most of the variation found could be attributed to the latter factor.

The tissue volume increased during a stadium; its value as given by a in formula 3 was always smaller than that of the immersion volume, but its rate of increase, value b, was always greater. This excess increase of tissue volume over immersion volume was accommodated by a decrease in the volume of the tracheal system. At an ecdysis the immersion volume was approximately doubled, but the tissue volume and density remained unchanged. The tracheal volume increased greatly, partly because of real growth and partly because of the absence of tissues pressing upon its air sacs. This increase in volume of the tracheal system " allowed " the immersion volume of the animal to increase at an ecdysis while the tissue volume and density remained constant. A diagrammatic representation of these changes is given in figure 3.

The significance of these changes in volume during the growth of the locust is best considered in relation to the events which occur at an ecdysis. The expansion of the body whilst the locust was casting its skin was caused by a swallowing of air which swells out the gut, pressing the blood and tissues against the folded integument and expanding this to its fullest extent (Duarte, 1939). The body was held in this fully expanded state until the integument had hardened and could retain its new form. The animal then relaxed, and the intersegmental membranes became folded beneath the sclerites, bringing about a decrease in volume. Even so, this final volume was about twice that before ecdysis. As has been pointed out, this new instar had about the same amount of tissue occupying the same volume as had the previous one. There must be some change in the body other than a decrease in tissue density which will occupy the extra volume produced by this rapid increase in size. This space was occupied by the swollen gut, but very shortly after ecdysis the gut shrank and the air sacs expanded filling the space created by gut shrinkage.

At an ecdysis the body was enlarged to accommodate the tissues and the food reserves that would be formed by the succeeding instar and which would accumulate at a constant rate throughout the stadium (fig. 1). The extra volume gained by the locust at an ecdysis lasting 15 minutes was not filled with tissues for a period ranging from 100–415 hours, depending on the duration of the stadium. Some means of dealing with this rapid increase in volume which could be slowly obliterated as the stadium proceeded and the obliteration of which would not adversely affect the insect has to be developed. In the locust the air sacs fulfilled this function. They increased in volume at an ecdysis and slowly decreased in volume throughout the subsequent stadium.

The experiments of Demoll (1927), Lee (1929) and McGovran (1931) have shown that air circulates through the tracheal system of Acridids, and that the air sacs play a part in pumping it in through the anterior spiracles and out through the posterior ones. It might be expected that this function would be impaired by the decrease in tracheal volume, but dissections showed that the air sacs occluded by the growing tissues could not aid in this circulation of air. A description and figures of the abdominal tracheal system are given by

Albrecht (1953) and should be referred to for further examination of this problem. They have been verified by dissection in female locusts. It is important to note that the abdominal air sac system is connected to the rest

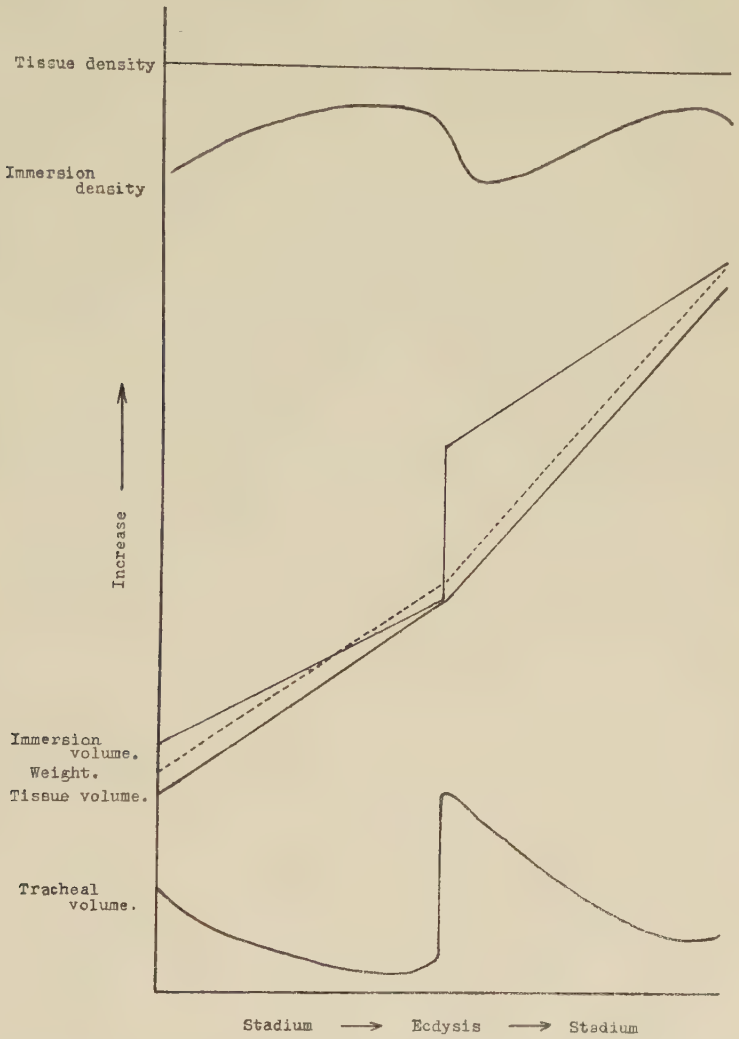


Fig. 3.—Diagrammatic representation of the changes in weight, volume and density which occur during a stadium and at an ecdysis.

of the tracheal system in such a manner that no amount of pumping by it could cause air to enter through the thoracic and leave through the abdominal spiracles. Lee (1929) showed that air could be taken in through the first abdominal spiracles but, although this would allow air to be pumped through the dorsal abdominal air sacs, it would not aid in pumping it through the other trachea. In the female, tracheae and tracheoles arise from these air sacs to

supply the dorsal fat body. It is unlikely that the dorsal air sacs were developed in response to excessive ventilation requirements of this tissue, since the tracheae supplying the similar ventral fat body do not possess air sacs. At all stages throughout the stadium it was noted that the tracheae and tracheoles arising from the dorsal abdominal air sacs contained injected fluid, so that occlusion of the air sacs did not prevent access to these tracheae from the spiracles. These air sacs are flattened structures, their lateral walls being thin and flexible, with their narrow anterior and posterior borders strengthened by semi-circular thickenings of cuticle, which, when the lateral walls are brought together under moderate pressures, were observed to keep open a conduit along the lateral margins of each air sac. It is through these conduits that the injected fluid reaches the dependent tracheae when the rest of the air sac is occluded and that air reached the dorsal fat body at all times during the stadium. In the male locust, the testes are supplied with tracheae arising from the dorsal air sac system (Albrecht, 1953). In this sex the dorsal abdominal air sacs may have a respiratory function, or air in sufficient quantity may reach the testes through the conduits without the aid of respiratory movements.

Because of its anatomical connections, its slow occlusion during a stadium and, in the female, the very small amount of tissue it supplied, it is suggested that the probable function of the dorsal abdominal air sac system is to take up the extra volume caused by the increase in linear size at an ecdysis, when the mass and volume of the tissue remain constant. It is, therefore, an adaptation for this purpose. The dorsal abdominal air sac system only is referred to here, the other air sacs in the body lie on the route air must take in passing from the spiracles to important tissues of the body, or between the thoracic and abdominal spiracles. These air sacs did decrease in volume, but they were never completely occluded during a stadium. They probably have the respiratory functions generally attributed to air sacs.

That the air sacs play an important part in the size increases occurring at an ecdysis has been suggested for *Lucilia sericata* Meig. by Evans (1935). He was able to show that the newly-hatched adult fly could not retain its shape if the abdominal spiracles were blocked, the air sacs under these circumstances not filling with air. Further, during adult life he observed that the abdominal air sacs greatly decreased in volume by the forward growth of the gonads pressing on them. The air sacs in *L. sericata* do not, like those of the locust, form a self-contained unit but are expansions of the lateral tracheae. They are, therefore, anatomically able to aid in air circulation. Their occlusion need not impair the efficiency of this function, for, providing the volume of the air sac does not become less than the volume of tidal air for a single respiration, no decrease in tidal air will occur. Indeed, in one sense the system may be more efficient as the volume of these air sacs decreases, because, as the volume of the air sacs approaches that of the tidal air, a larger percentage of air in the system will be changed at each respiration.

These changing relationships of tissue mass and volume to linear size during growth are common in insects. The accounts given of moulting in various insects suggest that different mechanisms have been evolved to permit rapid changes in the latter while the former remains constant. A comparison of these descriptions with each other and with the work described above suggests that these adaptations may be grouped as follows :

Group 1.—This comprises those insects in which only a small proportion of the integument is occupied by sclerotic plates which are not joined together to form a rigid framework. Examples are found amongst the soft bodied larvae of Endopterygote insects, where there is not so much an adaptation to meet this problem as an avoidance of it. Yagi (1926) measured the weight and volume of larvae of *Bombyx mori* at different times throughout each stadium. Comparison of his figures for samples taken before and after an ecdysis show little difference in immersion volume, although during an ecdysis the volume of the larvae is greatly increased, because the soft integument is able to fold down on to the tissues when the gut empties of air, leaving no enclosed space to be temporarily filled until the growth of tissues occludes it.

Group 2.—This comprises those insects in which a large proportion of the integument is occupied by sclerotic plates that may be fused to form a rigid framework. In these animals, as in those of the previous group, the body is expanded to its maximum size at an ecdysis by the swallowing of fluid into the gut, but when the animal relaxes a space is created within it which the tissues, remaining constant in mass and density, cannot fill. This space is formed because the sclerotic plates are larger than they were before the ecdysis and do not, because of their rigidity, collapse or fold when the internal body pressure relaxes. This situation is accentuated particularly if box-like structures such as the pterothorax are present. The substance used temporarily to fill this space provides a basis for subdivision within this group.

The locust may be taken as an example of the first subdivision, where the space is filled with air. The negative pressure created in the haemocoele when the gut shrinks causes the air sacs to expand, drawing air into themselves through the spiracles. As the stadium progresses new tissues press on these air sacs, occluding them and slowly occupying the extra space formed at the preceding ecdysis. In other insects it seems possible that air may be taken into other parts of the body. In the mosquito Marshall and Staley (1932) showed that when the adult emerges from the pupa, air is taken into the mid-gut, the gut diverticula at this stage being empty. When the mosquito is fully expanded air disappears from the mid-gut and appears in the gut diverticula, from which it tends to disappear when the animal feeds. Thus, at this time it would seem that the gut diverticula have the same function in the mosquito as have the dorsal abdominal air sacs in the locust.

The second subdivision contains those insects which take water into the body at the time of ecdysis, and appear to retain it throughout the succeeding stadium. Schafer (1923) found that in the nymph of *Anax junius* the weight was increased by the intake of water into the gut at the time of moulting, and that this water was absorbed into the haemocoele. Teissier (1931) recorded that in *Notonecta glauca* the animal's weight was increased at each moult by the uptake of water and that this gain in weight was retained. This is of some importance when considering the rate of growth of the tissues of these animals. If, as postulated, water taken in at an ecdysis is slowly replaced during the following stadium, then the true growth should be represented by an increase of weight equal to the amount of water taken in at an ecdysis plus the weight gained during a stadium, and not by the latter alone.

The figures obtained for the locust for the volume of the tracheal system show that in this animal the ratio of tracheal volume to body volume during

a stadium is not constant. Comparison between successive instars was only possible by choosing animals in an equivalent stage of development in each stadium. Towards the end of the stadium immersion volume and tissue volume are almost equal, and for all instars at this stage the ratio of the means of tracheal volume to body volume was 3·8 per cent. of the body volume. Krogh (1920) on *Dytiscus* and Demoll (1927) on *Melolontha* found the tracheal volume to be 10 per cent. and 39 per cent. of the body volume respectively. The value for the locust is 42 per cent. at the beginning and 3·8 per cent. at the end of the stadium. Without knowledge of the ages of the other species of insects whose tracheal volume has been measured a comparison cannot be made.

V. Summary.

(1) The changes in weight, immersion volume and tracheal volume that occur in the growing locust throughout the third, fourth, fifth and early part of the adult instar have been measured. From these measurements changes in the tissue volume and tissue density and in immersion density have been calculated.

(2) The tracheal volume was found to decrease during a stadium and increase at an ecdysis. The decrease in volume was due to the gradual occlusion of the abdominal air sacs by pressure of the growing tissues. Expansion at an ecdysis was due to real growth and to the absence of any tissue pressure on the air sacs.

(3) Integration of the changes measured and calculated showed that these changes in the volume of the tracheal system are an essential part of the events which take place at an ecdysis to allow an increase in linear size and in volume while the mass and density of the tissues remain constant.

(4) Investigations on the anatomy of the air sacs of the locust showed that the dorsal abdominal air sacs form a unit of the tracheal system which anatomically cannot play a part in the circulation of air to the body organs. These air sacs, which are occluded during a stadium, are thought to be an adaptation to facilitate the growth changes already described.

(5) The possible occurrence in other insects of structures which serve to " take up " the extra space produced within the insect's body by size increase at an ecdysis, and to allow for occlusion by growing tissues in the subsequent stadium, is discussed.

References.

Albrecht, F. O., 1953, *The Anatomy of the Migratory Locust.* London.

Deegener, P., 1904, Die Entwicklung des Darmcanals der Insecten währender der Metamorphose. *Zool. Jb.* (*Anat.*) **20** : 499–676.

Demoll, R., 1927, Untersuchungen über die Atmung der Insekten. II. *Z. Biol.* **87** : 8–22.

Duarte, A. J., 1938, Problems of growth of the African migratory locust. *Bull. ent. Res.* **29** : 425–6.

—— 1939, On ecdysis in the African migratory locust. *Agron. Lusitana, Lisbon* **1** : 22–40.

Eidmann, H., 1924, Untersuchungen über Wachstum und Hautung der Insekten. *Z. Morph. Ökol. Tiere* **2** : 566–610.

Evans, A. G., 1935, Some notes on the biology of the sheep blowfly, *Lucilia sericata* Meig. *Bull. ent. Res.* **26** : 115–22.

Keister, M. L., 1948, The morphogenesis of the tracheal system of *Sciara*. *J. Morph.* **83** : 373–422.

Krogh, A., 1920, Studien über Tracheenrespiration III. *Pflüg. Arch. ges. Physiol.* **179** : 113–120.

Kuhn, H. and Piepho, H., 1938, Die Reaktionen der Hypodermis und der Versonschen Drusen auf des Verpuppungshormon bei *Ephestia kuhniella* Z. *Biol. Zbl.* **58** : 13–51.

Lee, M. O., 1929, The function of air sacs in holopneustic insects. *Science* **69** : 334–5.

Marshall, J. F. and Staley, J., 1932, On the distribution of air in the oesophageal diverticula and intestine of mosquitoes. *Parasitology* **24** : 368–81.

Mather, K., 1943, *Statistical Analysis in Biology.* London.

McGovran, E. R., 1931, A method of measuring the tracheal ventilation in insects, and some results obtained from grasshoppers. *Ann. ent. Soc. Amer.* **24** : 751–61.

Schafer, G. D., 1923, The growth of dragonfly nymphs at the moult and between moults. *Stanford Univ. Publ. Ent.* **3** (4) : 307–37.

Teissier, G., 1931, Recherches morphologiques et physiologiques sur la croissance des insectes. *Trav. Sta. biol. Roscoff.* **9** : 29–238.

Tiegs, O. W., 1922, Researches on insect metamorphosis Pt. 1. *Trans. roy. Soc. S. Aust.* **46** : 319–527.

Wigglesworth, V. B., 1950, A new method of injecting the tracheae and tracheoles of insects. *Quart. J. micr. Sci.* **91** : 115–37.

Yagi, N., 1926, Analysis of growth curves of insect larvae. *Mem. Coll. Agric. Kyoto* **1**.

OBSERVATIONS ON SWARMING IN BRACONIDAE (HYMENOPTERA) AND CONIOPTERYGIDAE (NEUROPTERA).

By T. R. E. Southwood.

(Imperial College of Science and Technology, London).

It is well known that in the Ephemeroptera, many Formicidae and certain members of the Nematocera, notably the Culicidae, Chironomidae and Trichoceridae, large numbers of flying males form aggregations; these are mostly associated with pairing. The following observations have been made on groups where this type of behaviour is less often recorded.

Blacus ruficornis Nees (Braconidae).

At 5.45 p.m. B.S.T. on 26th August, 1954, large numbers of a Braconid were observed swarming at about five to eight feet above a swampy meadow near Flatford Mill Field Centre, East Bergholt, Suffolk. They were kindly identified as *Blacus ruficornis* Nees by Mr. A. W. Stelfox. The swarms were quite small, but many other individuals could be seen leaving the vegetation and flying up in a zig-zag manner to join the dance. Soon there were about 30 swarms over the meadow; they varied in size but generally contained something of the order of 100–300 individuals. The air was generally still but there were occasional gusts. When these occurred the swarms, which were roughly equidimensional, became much flatter and closer to the ground. Many individuals settled on the vegetation, running to the tops of the grasses and other plants at once; as soon as the gusts died away they rejoined the swarm. Unfortunately I had to leave the area at 6.30 p.m.; on my return at 8.0 p.m. swarming had ceased and no *B. ruficornis* could be taken by sweeping.

The field was revisited and swept at 10.30 a.m. the next day (27th August); once again no *B. ruficornis* were taken. At 5.35 p.m. that day there was no swarming, but at 5.45 p.m. it was again observed. Large numbers of individuals were seen leaving the vegetation and flying upwards to join the swarms. Some participants were seen to fall downwards rapidly; it was thought that these might be pairs that were copulating, but in the three cases where it was possible to follow these individuals they were found to be males and they rapidly climbed to the top of the grass and again rejoined the flight.

Aerial sweeps were made at 5.50 p.m., 6.20 p.m. and 7.5 p.m.; 135 individuals were taken, all of which were males. Careful observations were carried out through this period, but no definite evidence of mating could be seen. However, by 7.10 p.m. the number of swarms was reduced and the light was such that the individuals in one swarm could be seen very clearly. It was then possible to confirm what had been noted throughout the evening, namely that there were two distinct types of flight.

(1) *Vertical dance.*—The predominant movement (when viewed from the side) is vertical; the individuals move more slowly and are further apart than in the horizontal dance and, from below, they can be seen to move in a series of figures of eight.

(2) *Horizontal dance.*—The predominant movement is horizontal and very rapid, the individuals moving so quickly that they appear as a streak, especially when they turn. When this type of dancing commenced the individuals could be seen to come closer together so that the swarm decreased in size.

It might be expected that the more active horizontal dance occurs when a female enters the swarm, but there was no evidence for this. By 7.33 p.m. only one swarm remained and that was above my head. Three minutes later this dispersed. This tendency to dance over an object appeared to be marked only towards the end of swarming.

It seems that no other Braconid has been observed performing aerial dances, but those of *Blacus* were first described by Haliday (1836), who noted, in his original description of *B. tripudians*, that males danced in swarms like Chironomids. Subsequently swarms of this species have been observed by Benson (1944) and Hobby (1951), whilst Marshall (1889) noted similar behaviour in males of another species, probably *B. ruficornis*. Stelfox (1941, 1944) and Southwood (1952) have both recorded swarms of *B. ruficornis*, and Donisthorpe (1936) one of a species determined as probably *B. paganus* Haliday.

From these and the present observations certain generalisations can be made on swarming in *Blacus* spp. The swarms occur in the early evening, between about two and a half hours and half an hour before sunset, in both June (Donisthorpe, Benson) and August (Stelfox, Hobby, Southwood). The situations vary; Benson, Donisthorpe and Southwood observed dancing in small open spaces between trees, whilst at East Bergholt and at St. Weonards (Hobby) enormous swarms were seen over marshy ground. Benson observed larger individuals that he "took to be females" flying up into the swarm; both he and Stelfox found females in the samples collected. As other observers have found only males and in the present case it has been shown that dancing occurs on at least two successive evenings, perhaps the females partake only occasionally. It is hoped that further studies will elucidate this point.

Coniopteryx tineiformis Curtis (Coniopterygidae).

While collecting with Dr. A. M. Massee at Bookham Common, Surrey, on 4th July, 1954, I noted a swarm of small grey flies dancing about four feet above the ground and adjacent to a small hawthorn (*Crataegus monogyna* Jacq.). Two specimens were captured and proved to be males of this species, which is known to be attached to hawthorn (Killington, 1936). The swarm must have contained between 70 and 100 individuals, but whether, as in most other groups, these were all males or whether both sexes were represented was unfortunately not determined.

Killington (1936) remarks that many Neuroptera fly when thunderstorms threaten and quotes Donovan (1795) as the first to have recorded this phenomenon. On this particular occasion at Bookham Common a short, but heavy shower occurred a few minutes earlier (at about 2.0 p.m. B.S.T.); subsequently there was a storm with exceptionally heavy rain. However, this type of aggregation has not, it seems, been previously noticed in European Neuroptera, although Balfour-Browne (1956*a*) observed a large swarm of *Hagenomyia tristis* (Walker), a Myrmeleontid, in Transvaal. In this case the aggregation was seen about mid-day; it consisted of both sexes but no pairs

were found *in copula*. Subsequently, similar observations were recorded from South Africa, Rhodesia and Nigeria (Balfour-Browne, 1956*b*).

References.

Balfour-Browne, J., 1956*a*, [Exhibit note]. *Proc. R. ent. Soc. Lond.* (C) **20** : 8.

—— 1956*b*, [Exhibit note]. *Ibid.* **20** : 51.

Benson, R. B., 1944, Swarming flight of *Blacus tripudians* Haliday (Hym. : Braconidae). *Ent. mon Mag.* **80** : 21.

Donisthorpe, H., 1936, Dancing habits of some Braconidae. *Ent. Rec.* **48** : 84.

Donovan, E., 1795, *The Natural History of British Insects.* London. (Not seen).

Haliday, A. H., 1836, Essay on parasitic Hymenoptera. *Ent. Mag.* **3** : 20–45.

Hobby, B. M., 1951, [Exhibit note]. *Proc. R. ent. Soc. Lond.* (C) **16** : 53–54.

Killington, F. J., 1936, *A monograph of the British Neuroptera.* **1**. Ray Society, London.

Marshall, T. A., 1889, A monograph of British Braconidae. Part III. *Trans. ent. Soc. Lond.* **1889** : 149–211 (170).

Southwood, T. R. E., 1952, A swarm of *Blacus* (Hym. : Braconidae). *Ent. mon. Mag.* **88** : 45.

Stelfox, A. W., 1941, A new species of *Blacus* (Hymenoptera : Braconidae), with some notes on other species of the genus. *Proc. R. Irish Acad.* **46** (B) : 121–4.

—— 1944, The swarming flights of *Blacus* (Hym. : Braconidae). *Ent. mon. Mag.* **80** : 208.

THE ABRASION OF THE STERNAL SPATULA OF THE LARVA OF *DASYNEURA TETENSI* (RÜBS.) (DIPTERA : CECIDOMYIDAE) DURING THE POST-FEEDING PHASE.

By R. S. Pitcher.

(*East Malling Research Station, Maidstone, Kent.*)

[Communicated by Dr. A. M. Massee.]

The sternal spatula is a structure peculiar to the mature larvae of most, but not all, species of the family Cecidomyidae. It is a short chitinised rod whose lobed head protrudes from the ventral surface of the prothoracic segment. Since its discovery by Réaumur (1736–40), its unique appearance has excited the curiosity of many entomologists and during the past century a flood of opinions has been offered as to its function. Many of these views are conflicting and seem to be little more than speculations, but a few are based on definite evidence or careful observations relating to a particular species. It is not proposed to discuss the subject in detail but a brief summary of the principal opinions, with notes on the evidence offered or species studied, is given below.

Summary of Literature on the Function of the Sternal Spatula of Cecidomyid Larvae.

A. *Opinions Relating to the Feeding Phase.*

(1) *Use as an Aid to Feeding.*

(*a*) In woody tissues (fibres in the mine or lodged behind the spatula) : Eckel, 1903—*Retinodiplosis resinicola* (O.S.) ; Felt, 1913—*Monardia lignivora* (Felt).

(*b*) In leaf mines : Laboulbène, 1893—*Monarthropalpus buxi* (Geoff.).

(*c*) In abrading plant cells to extract sap at phase of maximum feeding : Réaumur, 1736–40 ; Kieffer, 1894.

(2) *Use as an Organ of Locomotion.*

(*a*) In crawling : Osten Sacken, 1862.

(*b*) In leaping : Giard, 1893.

(3) *Use as an Organ of Support in a Mine.*

Chaine, 1913—*Monarthropalpus buxi* (Geoff.).

B. *Opinions Relating to the Post-feeding Phase.*

(1) *Use as an Organ of Perforation.*

(*a*) In preparing pre-emergence holes for imago in woody galls, *etc.* (observations and comparative structure of spatulae) : Kieffer, 1894, 1900, and Sen, 1939—*Helicomyia saliciperda* (Dufour).

(*b*) In preparing a pre-emergence cap for imago in the cocoon (observation and comparative structure of spatulae and cocoon) : Kieffer, 1894, 1900—

Cecidomyia pini (De G.); Williams, 1910—*Retinodiplosis resinicoloides* (Williams),

(2) *Use as a Fulcrum for Reorientation of Larva within Cocoon.*
Enock, 1891 and Marchal, 1897—*Mayetiola destructor* (Say).

(3) *Use in Cocoon Construction.*
Williams, 1910—*Retinodiplosis resinicoloides* (Williams); Mik, 1891.

(4) *Use as an Organ of Locomotion through Soil.*
Kieffer, 1900 (quoting Giard, 1894, *unpublished*).

That objections can and have been raised to most of these theories is not surprising in view of the diverse habits of cecidomyid larvae. There is, however, general agreement that the spatula does not appear before the latter part of the feeding phase and in a few species, e.g. *Mayetiola destructor* (Say), not until feeding has ended. This fact tends to favour a post-feeding function, although use in the later stages of feeding in some species is not precluded. Of the possible post-feeding functions the preparation of a pre-emergence hole for an imago which would otherwise be entombed in a hard gall seems the most probable and has the support of several observers. Moreover, Kieffer and others have claimed that the best developed and most heavily chitinised spatulae are to be found in such species. There is less evidence for the preparation of pre-emergence caps in cocoons and hardly any for the other suggested functions.

The Function of the Sternal Spatula in *Dasyneura tetensi* (Rübs.).

Dasyneura tetensi, popularly known as the Black Currant Leaf Midge, is regarded by fruit-growers as a pest because of the damage it does to young leaves of black currant shoots. Midges first emerge from the soil in April and lay eggs in the tightly folded leaves around the growing point. The larvae feed on the upper surface of the leaves, preventing normal expansion of part or all of the lamina. There appear to be three larval instars whose major morphology agrees with those of *Thomasiniana theobaldi* Barnes (Pitcher, 1955). When fully fed the larvae crawl from the curled leaves and fall to the soil, which they penetrate to a depth of 1–2 cm. before pupating in a thin soft-walled cocoon, smooth within, but covered outside with loosely-attached soil particles. There are from two to four generations in a year; the winter is passed as a resting larva in a cocoon.

The sternal spatula appears at the second moult and thus is present during the latter third of the feeding phase and throughout the post-feeding phase. Its head is bilobed, the lobes being roughly triangular in shape and separated by a deep V-shaped suture (fig. 1*a*). From the nature of its biology *D. tetensi* does not need its spatula for any of the following tasks: (1) eroding a woody food medium; (2) crawling or leaping (it crawls readily in all instars and rarely leaps); (3) as an organ of support in a mine; (4) making a pre-emergence hole in a closed gall.

The feebler first and second instar larvae, which are not furnished with a spatula, appear to extract nourishment from the leaves quite readily. There seems, therefore, no reason to suppose that the spatula is essential for the feeding of the third instar, although it could presumably be used to supplement the chemical action of the larval secretions by some mechanical injury of the

leaf surface. There remain, however, a number of possible uses for the spatula in the post-feeding phase of larval life which will be discussed later.

In the course of biological studies on *D. tetensi* it was noticed that the spatulae of larvae within cocoons found below black currant bushes in the field had, in most cases, rounded lobes. The difference between these and those of larvae recovered from leaves was so striking that at first they were thought to belong to another species. Examination of spatulae of undoubted *D. tetensi* larvae which had entered the soil and made cocoons in the laboratory showed, however, that various degrees of rounding of the lobes of the spatulae had often occurred. It seemed, therefore, that the prepupal activities of the larva normally included some task which blunted the lobes of the spatula. The only comparable published observations which the writer has been able to find are those of Kieffer (1894), who suggested that differences he found in the spatulae of willow " shot-hole " midge larvae were due to wear occasioned by the preparation of a pre-emergence hole. In his 1900 monograph (p. 293), however, he retracts this theory as he found he had been dealing with two species, *Helicomyia saliciperda* (Dufour) and *H. pierri* (Kieffer), which have broad and narrow spatulae respectively.

Experimental Investigation of Wear in the Sternal Spatula of *D. tetensi*.

As it seemed quite possible that the local soil, a fine sandy loam derived from Hythe Beds, contained the abrasive agent responsible for the wear of the spatula, preliminary experiments were made with substances such as chalk, sand and carborundum, of sharply different abrasive qualities. Mature larvae were placed on each medium and recovered after cocoon formation, but prior to pupation. Examination of their spatulae lent support to this theory and two replicated experiments were therefore set up to obtain further evidence. Substantially the same techniques were employed in each. In experiment 1 small quantities of peat and field soil were prepared by screening through 60 mesh per inch sieves and about 25 per cent. of finely ground carborundum added to some of the soil to make a third medium. Approximately equal quantities of each medium were placed in glass blocks with a hemispherical cavity, lightly damped and their surface smoothed. Experiment 2 included two additional treatments, a 30-mesh sand/carborundum medium, designed to give maximum abrasion and, to assess the shape of the spatula before any abrasion had occurred, batches of untreated larvae were retained. For both experiments mature larvae were collected from curled black currant shoots and ten active specimens placed in each container. Most of the larvae buried themselves within a few hours but any which could not penetrate the medium within 48 hours were removed. After three days the contents of each container was washed through a 30-mesh sieve and cocoons and any free larvae collected, heated in 30 per cent. and preserved in 70 per cent. alcohol. Later the anterior ends of all larvae were removed and mounted in Berlese Fluid. Care was taken to ensure that all spatulae lay flat between the cover glass and slide, thus presenting a uniform aspect to the observer. The slides were placed in a microprojector and the outlines of the spatulae drawn at a magnification of $\times$ 555 (*i.e.* as in fig. 1). An index of curvature of the tip of each lobe was obtained by fitting one of a

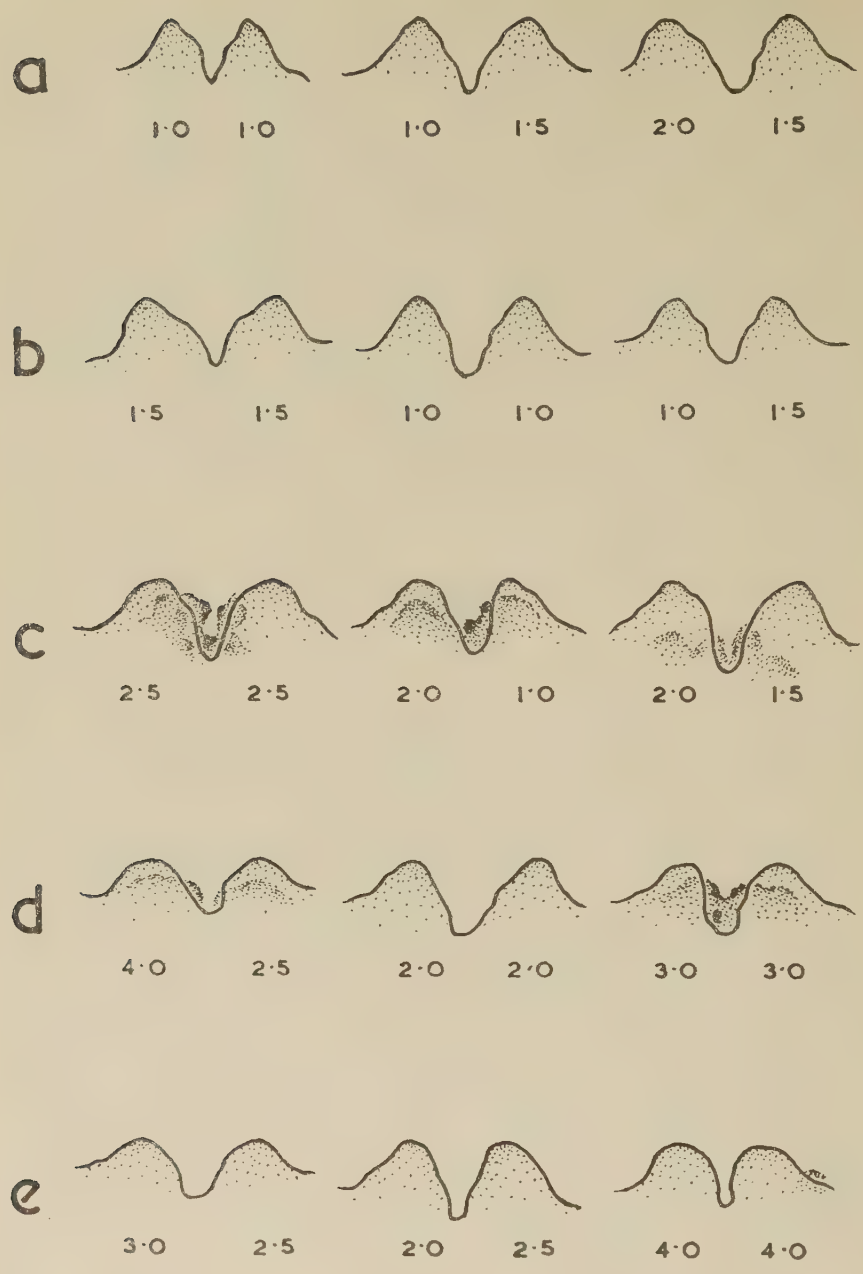


Fig. 1.—Heads of three spatulae typical of each treatment (× 555); the figure below each lobe is its index of curvature. Experiment 2, Replicate 3. (*a*) Larva from leaf. (*b*) Prepupa from peat. (*c*) Prepupa from soil.* (*d*) Prepupa from soil + carborundum.* (*e*) Prepupa from sand + carborundum. * Note debris between and behind lobes.

series of circles with radii from 1–6 mm. to these drawings. At first the data relating to larvae dissected out of cocoons and those found free in the medium were kept separate but, as no significant differences were found, these figures were combined to obtain the mean curvatures given in Table I. It was also found that substantial amounts of some of the media became lodged between and behind the lobes of the spatulae (fig. 1*c* and *d*). Records of this, presented as the percentage of spatulae in each treatment whose V-shaped suture was more than half filled with debris, are also given in Table I. The figures of mean curvature show differences significant at the 0·1 per cent. level, except where they are bracketed. Three typical spatulae from each treatment are shown in fig. 1.

TABLE I.—*Rounding of lobes and accumulation of debris in sternal spatulae of larvae of* Dasyneura tetensi.

	Medium :				
	Nil.	Peat.	Soil.	Soil + carborundum.	Sand + carborundum.
Experiment 1 (seven replicates, S. D. 0·59)					
Mean index of curvature	.	1·54	3·43	3·07	.
% with debris . . .	.	0	41	18	.
Experiment 2 (five replicates, S. D. 0·24)					
Mean index of curvature	1·42	1·37	2·20	2·37	2·51
% with debris . .	0	0	26	16	0

DISCUSSION.

Differential wear of the spatula was clearly demonstrated by both experiments. In a soft medium, such as peat, the lobes suffered little or no abrasion during the post-feeding phase, whereas in all other media significant wear occurred. The addition of carborundum to soil had little effect, nor did the substitution of sand for soil, but a mixture of sand and carborundum caused slightly more wear than did soil alone. The frequent presence of substantial amounts of soil under the spatulae suggests a shovelling or scraping action and its virtual absence in media containing no soil probably reflects differences in the stickiness of the medium rather than in function of the spatula.

There seems little doubt, therefore, that in *D. tetensi* the spatula performs some mechanical task which is closely concerned with the medium in which the cocoon is made. In the absence of further evidence the precise function of the spatula can only be surmised, but most probably it is one or more of the following, all of which have at one time or another been suggested for other cecidomyid species.

(1) *In Tunnelling in the Soil to Reach a Suitable Pupation Site.*

This seems to be the operation most likely to cause wear or lodgement of debris behind the lobes. The structure and attitude of the spatula suggest an active digging function but it is also possible, as suggested by Barnes (*in litt.*),

that wear could be caused and debris accumulate incidentally as the larva forces its way through closely-packed soil by means of body movements. The absence of any significant difference between the wear of spatulae of larvae found in cocoons or free in the media suggests that the main wear occurs before cocoon formation, but this evidence is not conclusive as some of the free larvae may have made cocoons which were ruptured during the sieving process.

(2) *In Making the Cocoon.*

This, also, is a feasible explanation. Soil could easily become lodged under the spatula during the excavation of a pupal cell and the early stages of coccon making, but it seems unlikely that such relatively light work could wholly explain the extreme rounding of the lobes (to index 6) which occurred in some cases.

(3) *In Preparing an Exit from the Cocoon for the Imago.*

It is doubtful if this could be the sole explanation as the cutting of the cocoon would be a slight task, unlikely to cause much wear of the lobes. Moreover, in so doing the spatula would not come into contact with free soil particles, as those attached to the outside of the cocoon are embedded in a matrix secreted by the larva and unlikely, therefore, to become lodged behind the lobes of the spatula. Examination and testing of many cocoons has produced no evidence of a deliberately prepared weak spot or cap and the pupa is furnished with chitinised cephalic horns which appear quite capable of breaching the cocoon unaided.

Of the published theories on a post-feeding use of the spatula there remains only the use as a fulcrum for reorientation of the larva in its cocoon. In *D. tetensi* there are few restrictions on attitude or position of the larva and there seems to be no reason why it should regularly wish to alter its first choice. In any case, such an operation is unlikely to cause marked wear of the spatula.

The above observations apply only to *D. tetensi* but it is quite possible that other species which pupate in the soil make comparable use of their spatula. Proof of this should be readily obtainable in species with pointed-lobed spatulae, but more difficult in those whose spatula is rounded even when first formed. This finding does not in any way contradict prior evidence or observations on the use of the spatula for other functions in other species and, indeed, it would be futile to postulate an identical use for the spatula in all species. Doubtless the spatula originally met some particular need of an ancestral cecidomyid species but there seems to be no reason why, once present, it should not be used for any task for which it is suited and which the biology of its owner demands. In fact, by demonstrating mechanical abrasion of the spatula in one species the above experiments lend indirect support to those who claim that this organ is used by other species for heavy tasks such as the preparation of pre-emergence holes in galls or as an aid to the feeding of older larvae in woody plants.

Summary.

Experimental evidence shows that the rounding of the lobes of the sternal spatula of larvae of *Dasyneura tetensi*, which frequently occurs in the post-feeding phase, can be closely correlated with the abrasiveness of the medium

in which pupation takes place. It is, therefore, suggested that in this species the spatula is regularly used in digging or otherwise manipulating the soil prior to pupation.

Acknowledgments.

The writer wishes to thank Drs. A. M. Massee and H. F. Barnes for advice and for criticism of the paper, Dr. M. Cohen for examining some field soil and Mrs. C. Adlam for assistance with the experiments.

References.

Chaine, J., 1913, La cécidomyie du buis, *Monarthropalpus buxi* (Lab.),morphologie, biologie, dégats, traitement. *Ann. Sci. nat.* (*Zool.*) **17** : 269–361.

Eckel, L. S., 1903, The Resin Gnat *Diplosis* and three of its parasites. *Ent. News* **14** : 279–84.

Enock, F., 1891, The life-history of the Hessian Fly (*Cecidomyia destructor* Say). *Trans. ent. Soc. Lond.* **1891** : 329–66.

Felt, E. P., 1913, A study of Gall Midges, I. *Bull. N.Y. State Mus.* **165** : 127–226.

Giard, A., 1893, Note sur l'organe appelé *spatula sternalis* et sur les tubes de Malpighi des larves des cécidomyies. *Bull. Soc. ent. Fr.* **1893** : 80–84.

Kieffer, J. J., 1894, Sur le rôle de la spatule sternale chez les larves de cécidomyes. *Ann. Soc. ent. Fr.* **63** : 36–44.

—— 1900, Monographie des cécidomyides d'Europe et d'Algérie. *Ann. Soc. ent. Fr.* **69** : 181–472.

Laboulbène, A., 1893, Communication sur la spatule sternale et sur les tubes de Malpighi des larves cécidomyies. *Bull. Soc. ent. Fr.* **1893** : 74–75.

Marchal, P., 1897, Les cécidomyies des céréales et leur parasites. *Ann. Soc. ent. Fr.* **66** : 1–105.

Mik, J., 1891, Ueber Cecidomyiden. *Wien. ent. Ztg.* **10** : 1–3.

Osten Sacken, B. R., 1862, On the habits of the Cecidomyidae. *Mon. Dipt. N. Amer.* **1** : 179–98. Washington.

Pitcher, R. S., 1955, The larval instars of some gall midges of the genus *Thomasiniana* Strand, E., 1916 (Diptera : Cecidomyidae). *Proc. R. ent. Soc. Lond.* (A) **30** : 97–102.

Réaumur, R. A. F. de, 1736–40, *Mémoires pour servir à l'histoire des Insectes*, Vols. II–V. Paris.

Sen, P., 1939, On the function and development of the sternal spatula in the Cecidomyidae or Gall Midges as exemplified by *Rhabdophaga saliciperda* Duf. *J. Morph.* **65** : 1–16.

Williams, F. X., 1910, The anatomy of the larva of *Cecidomyia resinicoloides* Williams. *Ann. ent. Soc. Amer.* **3** : 45–60.

THE PRESENCE OF COREMATA IN *CREATONOTUS GANGIS* (L.) (LEPIDOPTERA : ARCTIIDAE).

By H. T. Pagden.

Introduction.

Coremata, plural of corema, are defined by de la Torre-Bueno (1950) as "specialized scent-tufts near the end of the abdomen of certain male Lepidoptera", a description which leaves one in some doubt whether they are scent-producing or scent-disseminating, whether internal or external, under control or involuntary. They are, in fact, glandular, internal and, apparently, voluntarily eversible.

So far as I am aware, the presence of coremata in the moth *Creatonotus gangis* (L.) has not previously been recorded, and I believe that I am also correct in stating that their extrusion under natural conditions has not so far been recorded in those moths in which these structures are known to occur. The following observation and accompanying photographs may, therefore, be of some interest.

Observation.

In Penang, on the night of 11th August, 1955, while pinning and labelling some Hymenoptera collected that day, my attention was attracted to an object on the wall of the room and distant about seven yards from where I was working. The object was in shadow and, seen in profile, appeared to be a small grasshopper with its hind-legs cocked up. I finished what I was doing before going to investigate and, although I made no note of the time, I estimate that it was about ten minutes before I got up and went to look more closely.

The object proved to be a specimen of a very common moth, *Creatonotus gangis* (L.), which often comes to light at certain times of the year, but it had the most remarkable structure extruded from near the apex of the lower surface of its abdomen ; it was this structure which had, seen from a distance and in poor light, given me the impression of the cocked-up hind legs of a grasshopper ; the black markings on the wings, the ground colour of which was almost the same as the wall, gave the impression of the body of a slender insect such as a grasshopper.

No time was wasted in detailed observations as it seemed to me that the incident was so remarkable that a photographic record was of the utmost importance, and I therefore prepared my camera as rapidly as possible and was lucky to obtain the three pictures which accompany this note (Plate I, a, b, c).

Preparations to photograph the insect took at least five minutes, probably nearer ten minutes, for the equipment had to be fetched from special storage upstairs ; the standard Leica lens had to be removed and a reflex housing with telephoto lens and three extension rings substituted, and the whole mounted on its tripod ; batteries had to be inserted in the electronic flash apparatus, after which there was a wait for the condenser to charge up before starting to shoot. There was an interval of about one minute between flashes because the

batteries (6 × 30-volt hearing-aid dry batteries) were not in good condition and it took some time for the condenser to become re-charged.[1]

Immediately after the first picture had been taken the moth started to retract this structure, which was almost half withdrawn by the time that the second exposure could be made, and nearly completely withdrawn when the last picture was taken.

After taking these photographs the moth was captured and killed, and a search of the room was made to see if there were any other specimens present. I guessed, quite wrongly as I discovered when I came to pin the specimen, that the insect which I had photographed was a female and that the structure which I had observed was an eversible scent gland for " calling " the male. No other specimens were found in the house that night, but there was a single specimen on the following night and one or more on most subsequent nights for the next month, after which observations ceased as the lease on my house expired and I had to leave.

Examination of Other Specimens.

As stated above, the specimen photographed was a male. A number of specimens collected during the month following the observation just recorded were dissected and it was found that coremata were present only in males, thus completely disposing of the theory which I had at first adopted.

A number of living specimens were collected and kept under observation, either separately or several together, in glass tubes of $1\frac{1}{2}$-inch diameter, and a watch was kept on other specimens attracted to light and resting on the walls of the room, but no other specimen was seen to extrude its corema.

Discussion.

The question which immediately presented itself to me was why, during a period of nearly 28 years in Malaya, I had never seen any other specimen of this very common moth indulge in this remarkable display. Could it be that I was unobservant, and that others had seen this display but thought it to be of common occurrence and not worth reporting? The most likely people to answer this question were the locally-born staff of the Division of Entomology of the Department of Agriculture, and I accordingly enquired from them whether any of them had ever seen anything of this nature. None of them had ever seen anything like it. It seems, therefore, that the natural extrusion of coremata, at least in *Creatonotus*, must be of rare occurrence.

Berlese (1907) seems to have considered similar structures found in the males of certain species of *Spilosoma*, *Arctia* and *Leucarctia* to be repugnatorial in function, but no evidence in support of this, other, perhaps, than the human sense of smell, seems to have been adduced. Berlese states that these organs occur in males only, or in both sexes, but de la Torre-Bueno (1950) states that they occur only in male Lepidoptera.

Creatonotus gangis appears to be distasteful, in both sexes, to the common house gecko, *Hemidactylus frenatus*, for I have never seen a single example

[1] These apparently trivial details regarding time are given because they show that the corema must have been extruded for at least 18 minutes and perhaps for 23 minutes after I had first noticed something strange on the wall. It would probably not be far wrong to guess that this " display " lasted for at least half an hour.

attacked by this voracious lizard. *H. frenatus* will approach the moth but generally turns away when a few inches from it and, even when it approaches more closely, it never seems to seize it before recognising it as something distasteful. The colouring of *C. gangis* is common to both sexes and is distinctly aposematic. If the coremata are repugnatorial in function one would expect to find them in both sexes, since both seem to be distasteful, but if confined to one sex it seems more likely that the female would be the privileged one. Also, if their function is repellent, one might expect them to be extruded much more frequently than seems actually to be the case. Furthermore, would it be necessary to extrude the corema for a period of 20–30 minutes in order to make use of its repellent function and, if so, why has this not been observed on many occasions?

Is the function of the corema sexual? If it is, it seems unlikely that it produces a scent which attracts the females from a distance, for no assembling has been observed in this species. It may also be noted that the antennae of the sexes are similar, both being setaceous.

If the function of the corema is to stimulate the female after the sexes have come together, it seems reasonable to enquire why not a single other specimen of this moth was to be found in the house when the display which I witnessed took place, for if its function is to stimulate the female to perform the sexual act the physical presence of a female would seem to be necessary in order to initiate the display.

Finally, numbers of specimens were kept under observation during the month following this first observation, some being free, some confined singly and some confined together, and yet the display was not repeated.

Historical Notes.

I am indebted to Mr. E. O. Pearson, Assistant Director, Commonwealth Institute of Entomology, to whom I sent copies of my photographs, for making an extensive search of the literature and for preparing the notes which follow :

" The earliest reference that I have been able to find to any structure appearing to correspond with those in the photographs of the male of *Creatonotus gangis* is that of Berlese (1907) to the occurrence in *Arctia* and related genera of a single pair of extensible organs situated at the end of the abdomen (the exact spot ill-defined). He describes these organs as in the form of a sac, very fine and hairy, of a reddish or orange colour, fleshy and sometimes very long, and states that they occur in the males only or in both sexes, and give off a very intense odour, sometimes unpleasant, and are considered as repugnatorial (*Spilosoma virginica, Arctia virgo, Leucarctia acraea*, etc.).

" The name *corema* (pl. *coremata*) for organs of this nature was first published by Prout (1912), who acknowledged it as having been provided for him by Burrows and Pierce, and defined by them as the extensible organ bearing a brush of long hairs, springing from the dorsal [sic] extremity of the eighth abdominal segment and above the junction with the tegumen. Pierce (1914) himself, describing the abdomen of the Geometridae, says that the seventh segment is sometimes highly developed, being produced on either side as an extensible pouch or bag clothed with hairs, these bags being called the coremata.

" Janse (1932), speaking of the abdomen of the Heterocera, says that the seventh or the ninth sternite may have eversible sleeve-like bags (*coremata*), sometimes of great length and covered with hairs ; he adds that this pouch no doubt serves as a scent container and distributor and can readily be evaginated by injection with a pipette. His fig. 9, of the generalised moth abdomen, shows the coremata arising apparently from the fold between sternites 7 and 8 and also (rather vaguely) from the base of the valves.

" Viette (1948) describes the coremata as occurring most often on the eighth segment, but quotes Janse as saying they are found on the seventh.

" Mr. N. C. E. Miller, of the Commonwealth Institute of Entomology, has drawn my attention to the fact that organs that appear to have the same nature have been described by Bethune-Baker (1925) from a number of species of the Arctiid genus *Rhodogastria*, but this author's description and photographs show these to arise from the outer surface of each of the valves or claspers of the male genital armature, folding back telescopically into a depression in the latter. The detailed structure is, however, exactly similar to the organs of *Creatonotus*, the surface being covered in small tubercles from each of which springs a long, wavy slender hair. Bethune-Baker states that these organs are scent-sacs, but adduces no evidence to show this, other than a strong odour said to characterise specimens of the genus. Eltringham (1927) described a brush organ in the common Agrotid, *Laphygma frugiperda* S. & A., that he likened to the structures found in *Rhodogastria*, and that consisted of a bladder-like lobe at the base of each clasper in the male, from which arose a brush of long, fine scales.

" In the present case, it seems clear from the succession of photographs of the organ of *Creatonotus gangis* that the hairs that cover the surface of the extensible processes will have the appearance of a brush when the latter are completely telescoped, and when the underside of the abdomen of the male is examined these brushes can be seen apparently emerging from between sternites 7 and 8. If all the body scales are scraped away it can be seen that there is a pronounced cavity between these sternites, due to the fact that segment 8 is much smaller than 7, and that the brushes are accommodated in this cavity.

" If the whole abdomen is lightly potashed, the organ can be extruded and can be seen to be clothed with fine hairs, each arising from a small tubercle. The process itself arises apparently from the intersegmental membrane between sternites 7 and 8, or possibly from the anterior lip of sternite 8 itself ; it is difficult to see whether the chitinous median flange that supports the organ is really a part of the seventh or eighth sternite (Plate I, D).[2]

" Although these organs have been named and appear to be quite widely found in the Lepidoptera, little attention seems to have been paid to them, either as regards their possible taxonomic value (except, perhaps, in the case of Prout [q.v.]), or with a view to discovering their real function, and it has not been possible to find a single reference to anyone having observed them in a state of extrusion in nature. Chrétien (1926), however, gives a detailed account of how, in killing a number of males of *Diacrisia menthastri-lubricipeda*

[2] The preparation here photographed was kindly made by Dr. I. W. B. Nye, of the Commonwealth Institute of Entomology, from a specimen of *C. gangis*, believed to be from Ceylon, in the British Museum (Natural History), B.M., 1927–341, genitalia slide 419).—E. O. P.

(Arctiidae) that were attracted to a light trap he was operating in the Pyrenees in June 1923, by pinching them between thumb and forefinger, he noticed that he had thus accidentally caused the extrusion of an organ, which he figures as emerging between the last two abdominal sternites, and which is unquestionably the same organ as that seen in *Creatonotus*. Chrétien was, however, apparently not aware that such an organ had been given a name.

" The present experience and photographs thus seem to be unique."

References.

Berlese, A., 1907, *Gli Insetti*, Fasc. **18–20** : 541.

Bethune-Baker, G. T., 1925, On the scent-sacs in the genus *Rhodogastria*. *Trans. ent. Soc. Lond.* **1925** : 321–8.

Chrétien, P., 1926, Organe évaginable de *Diacrisia* (*Spilosoma*) *menthastri-lubricipeda*. *Amat. Papillons* **3** : 65–71.

Eltringham, H., 1927, On the brush organs in the Noctuid moth, *Laphygma frugiperda* Sm. and Ab. *Trans. ent. Soc. Lond.* **75** : 143–6.

Janse, A. J. T., 1932, *Moths of S. Africa* : 22, fig. 9.

Pierce, F. N., 1914, *Genitalia of the Geometridae* : xxiv.

Prout, L. B., 1912, Lep. Het. Fam. Geom. Subf. Hemitheinae. *In* Wytsman, *Gen. Ins.* **129** : 6.

Torre-Bueno, J. R. de la, 1950, *A Glossary of Entomology*.

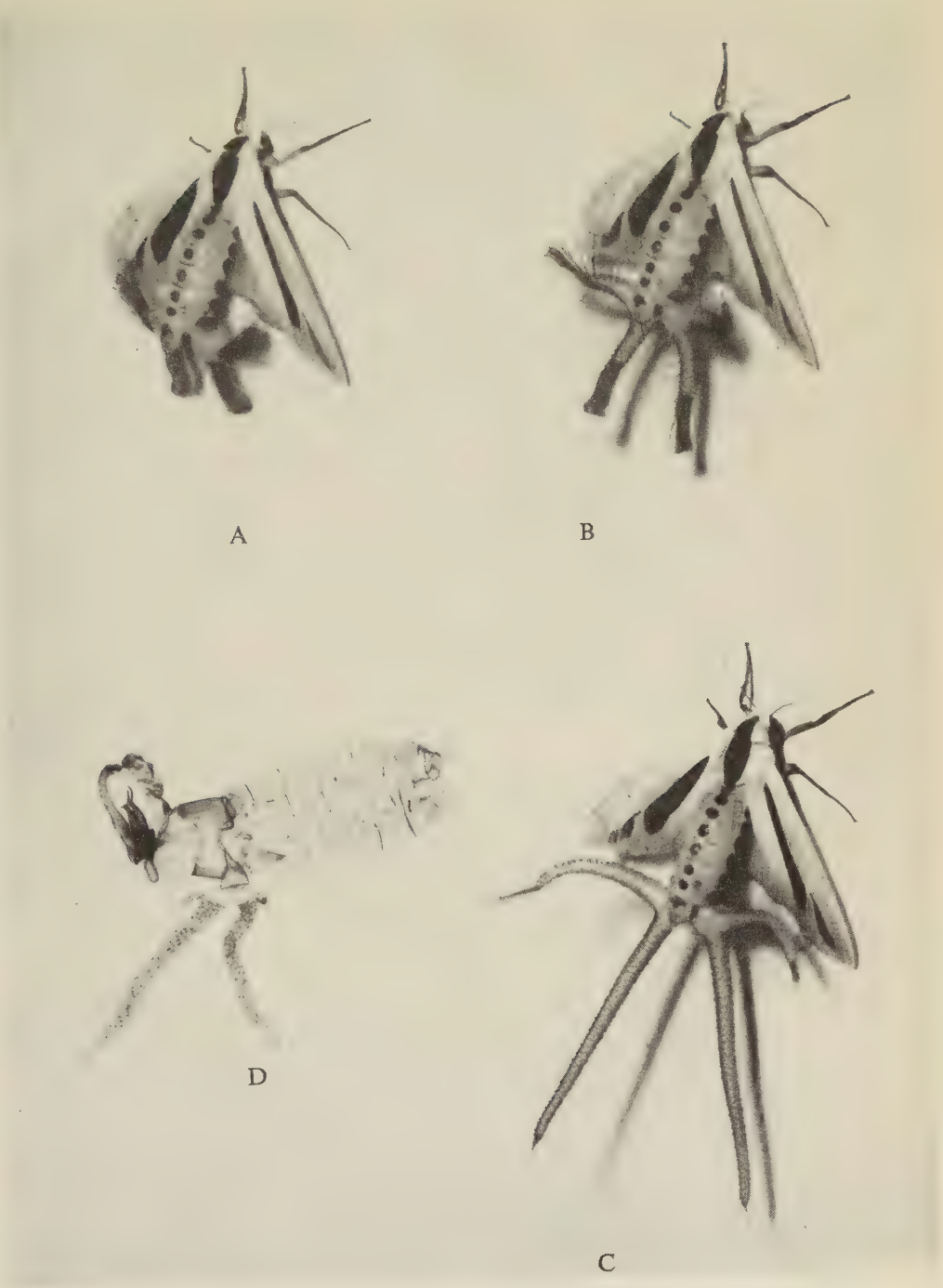
Viette, P., 1948, Morphologie des genitalia mâles des Lépidoptères. *Rev. franç. Ent.* **15** : 141–61.

PLATE I

Coremata of *Creatonotus gangis* (L.).

Figs. a–c.—Stages in the retraction of the coremata (the photographs are here arranged in the reverse of the order in which they were taken).

Fig. d.—Preparation of whole abdomen. Note that in this specimen, the paired digitate processes are of very unequal length.



Coremata of *Creatonotus gangis* (L.).

H. T. Pagden.

Adlard & Son, Ltd., Dorking.

SOME NOTES ON *GRYPIDIUS EQUISETI* F. (COL.: CURCULIONIDAE) WITH A DESCRIPTION OF ITS LARVA.

By E. M. Cawthra.

(*Department of Zoology, University of Glasgow*).

[Communicated by J. W. H. Lawson].

Grypidius equiseti F. is a phanerognathous weevil belonging to the tribe Erirrhinini of the subfamily Erirrhininae. The adult anatomy does not appear to differ greatly from other Curculionids seen or described by other authors (figs. 1–13). The unusual tegminal cap-piece (fig. 11, *T*) is typical of the tribe Erirrhinini, many of which feed on aquatic or semi-aquatic plants. The sex ratio appears to be even, since seven of the fifteen adults dissected were male and eight female.

Distribution.

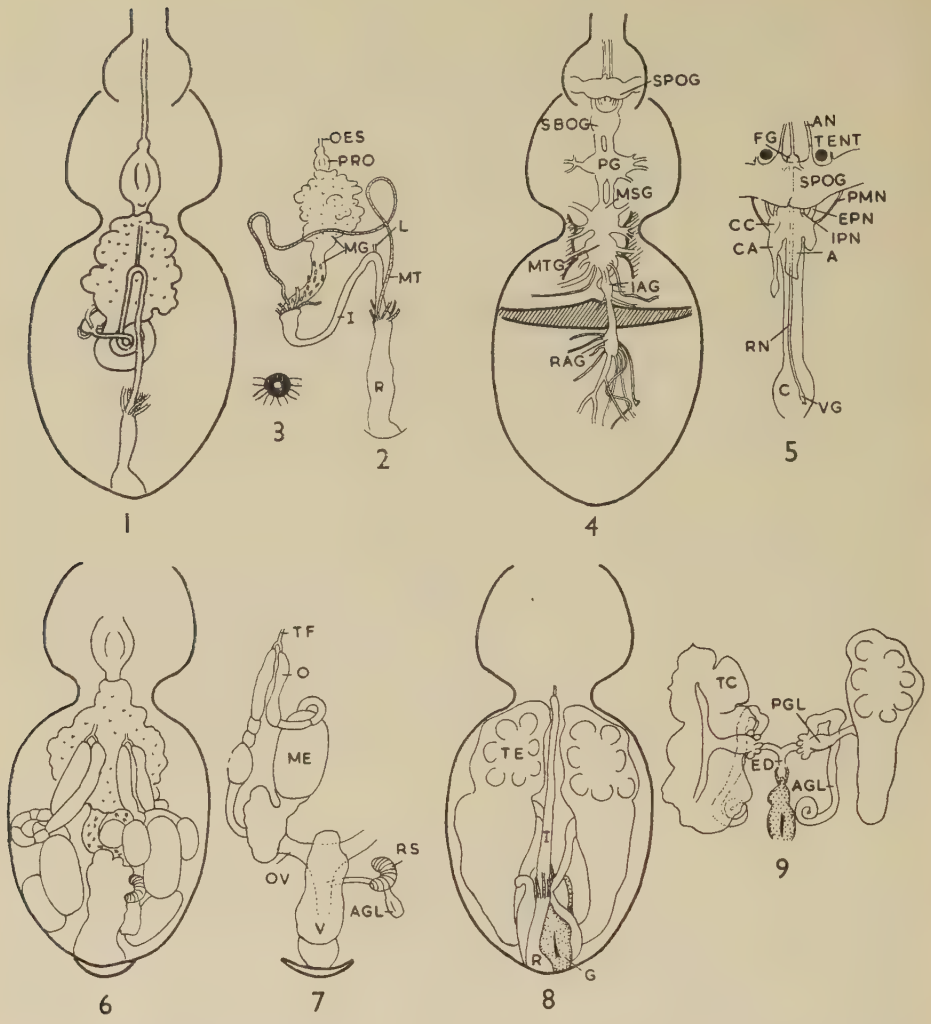
Locations for *Grypidius equiseti* given in the *Coleopterorum Catalogus* are Central Europe, Siberia and North America. According to Hustache (1930) it is common throughout France; Fowler (1891) writes, "It is rarely common but apparently widely and generally distributed throughout England and Wales . . . Scotland local, Solway and Forth districts." I have found it at four different localities within Glasgow city boundary, and there are also unpublished records of its occurrence at Barr and Ayr (Ayrshire) and Crookston (Renfrewshire) in the note-books of Fergusson and Stevens in Glasgow University Library.

Habits.

I have not seen it fly nor could I induce it to do so even by raising the temperature to 74° and placing several adults on an unsuitable plant (*Epilobium angustifolium*) or by shaking them off a fairly high plant. Instead of releasing their wings they drew in their appendages and were in consequence undamaged by the fall. The elytra of dead specimens are opened with difficulty and the wings are weakly veined (fig. 10). It appears that the weevils do not fly in this area unless during a very short interval after emergence from the pupa, and that the means of dispersal is walking.

Miss Jackson (1933) found that in the north of Scotland there was a much greater proportion of the flightless to normal forms of the weevil *Sitona hispidula*, than occurs further south. My observations appear to have been made near the northern limit of the British distribution of *G. equiseti*, and it would not be safe to conclude from them that it is flightless throughout its entire range.

Bargagli (1884) wrote of *G. equiseti*, "Fabricio states that it is found in England on *Equisetum arvense*, and in Scandinavia Zetterstedt says it can be found under stones, in low grass, in dry sandy regions in May and June. In Sweden the same author says it is common on *E. arvense*. In Austria it lives on damp grasses. In northern Italy it has been seen on *E. palustre*.



FIGS. 1–9.—*Grypidius equiseti* F. (1) Digestive system, *in situ*. (2) Digestive system. (3) Transverse section at junction of mid- and hind gut showing the origin of the six malpighian tubules. (4) Central nervous system. (5) Sympathetic nervous system. (6) Female reproductive system *in situ*. (7) Female reproductive system. (8) Male reproductive system *in situ*. (9) Male reproductive system.

A, aorta ; 1*AG*, first abdominal ganglion ; *AGL*, accessory gland ; *AN*, antennary nerve ; *C*, crop ; *CA*, corpus allatum ; *CC*, corpus cardiacum ; *ED*, ejaculatory duct ; *EPN*, external paracardiac nerve ; *FG*, frontal ganglion ; *G*, genitalia ; *I*, intestine ; *IPN*, internal paracardiac nerve ; *L*, ligament ; *ME*, mature egg ; *MG*, mid-gut ; *MSG*, mesothoracic ganglion ; *MT*, malpighian tubule ; *MTG*, metathoracic ganglion ; *O*, ovariole ; *OES*, oesophagus ; *OV*, oviduct ; *PG*, prothoracic ganglion ; *PGL*, prostate gland ; *PMN*, paracardio-maxillary nerve ; *PRO*, proventriculus ; *R*, rectum ; *RAG*, remaining abdominal ganglia ; *RN*, recurrent nerve ; *RS*, receptaculum seminalis ; *SBOG*, sub-oesophageal ganglion ; *SPOG*, supra-oesophageal ganglion ; *TC*, testicle ; *TE*, testis ; *TENT*, tentorium ; *TF*, terminal filament ; *V*, vagina ; *VG*, ventricular ganglion.

Priazolli has seen it on *E. vernale* on river banks in the Alps." (My translation). The latter species could not be traced but is probably a synonym of *E. arvense*. Fowler (1891) and Hustache (1930) say that it is to be found on *E. arvense* and *E. palustre*.

On extensive areas of *E. fluviatile* at Possil Marsh (Glasgow) and *E. sylvaticum* at Mugdock Wood (Dunbartonshire) no trace of *Grypidius* or its characteristic feeding scars was found. The stem of these species, especially the former, is probably too thin to provide feeding space for the larvae. When the adults were given a choice of *arvense* or *sylvaticum* they both fed on and oviposited in the *sylvaticum*, but to a much smaller extent than *arvense*. *E. hyemale* (Kelvingrove, Glasgow) and *E. pratense* (Falls of Clyde, Lanarkshire, and Saffron Walden, Essex) were examined but neither *Grypidius* nor its feeding scars were found. When it was given a choice of *hyemale* or *pratense*, and *arvense* its feeding was largely, and its oviposition entirely, restricted to the last-mentioned species.

Thus it seems that *Grypidius* is not only unable to fly but, in addition, is confined to two species of *Equisetum*. Although *Equisetum* on roadsides is subject to frequent scything, this need not annihilate the weevil. Only eggs and larvae still in the aerial shoots will die at each felling. But, as there is a long oviposition period in the field and plants are rarely cut down before mid- or late summer, some of the larvae will probably have already penetrated the rhizome safely below ground.

Fergusson's earliest record of *Grypidius* is of one specimen found at Barr (Ayrshire) on 14th April, his latest an unspecified date in July. On 29th May, I found numerous adults in the University grounds, and the last adult was found on 30th July. It is probable that adults could still have been found in the field after that date, as five survived in the laboratory until 22nd October.

Behaviour of Adults.

The Equisetales support few phytophagous insects, no doubt owing to the deposit of silica in the epidermis which makes it abrasive to most insect mouth-parts. *Grypidius*, however, has strongly pointed mandibles which enable it to break through the armoured layer to the succulent underlying vessels. While feeding on the vascular tissue a small area round the tip of the rostrum becomes slightly brown.

When old *Equisetum* stems were being removed from the cage, a weevil occasionally dropped off and lay motionless with legs and antennae flexed in towards the body. This state of reflex immobility was so readily induced that I tried an experiment similar to that of Fabre on *Scarites gigas*. Immobility was induced by dropping the beetle from a height of about 5 cm. on to its back. This could last from 20 seconds to over a minute, then the beetle began to recover. This process was so slow, however, that it might be 7 minutes before the beetle eventually turned over and moved away. In a fairly typical case the initial immobility lasted 50 seconds, then the mandibles opened and closed. After another 70 seconds they moved again. After 10 seconds more, the tarsus of the left mesothoracic leg and then the whole of one of the metathoracic legs flexed; 25 seconds later the antennae quivered. A further 50 seconds of immobility ensued, then the other metathoracic leg and the mouth parts moved; 30 seconds later all the legs flexed and antennae and mouth

parts quivered, and 60 seconds later the tarsi quivered slightly. Then after 40 seconds all the legs flexed and 30 seconds later they were kicked violently and the beetle turned over fully recovered, after a total time of 6 minutes 5 seconds.

Fabre found that when he immobilised *Scarites gigas* immediately on its recovery, it took successively longer periods to recover and eventually could not be induced to lie still. *Grypidius*, however, took successively shorter periods to recover, as can be seen from the two typical series below :

(1) Duration of first period of immobility (*i.e.* from dropping on its back until it turned over)—4 minutes, of second—1 minute 30 seconds, and of third —20 seconds. After this it would not lie still.

(2) Duration of first period of immobility—3 minutes 5 seconds, of second—1 minute 25 seconds, of third—50 seconds, and of fourth—25 seconds. After this it would not lie still.

It was found that weevils narcotised with ethyl acetate lay in similar positions to weevils in thanatosis and, moreover, showed the same sequence of movements in their recovery. This might be taken as supporting Fabre's suggestion that beetles in a state of thanatosis were in fact " unconscious ". It is remarkable how readily thanatosis is induced in *Grypidius* on its food plant in the field. The slightest movement in the vicinity may cause the weevil to drop off but with frequent handling in the laboratory they became much less sensitive. This thanatosis reflex is very widespread in Coleoptera and doubtless has survival value in enabling them to escape from predators, particularly birds.

Observations were made on the laboratory stock of *Grypidius* at midnight, 3 a.m. and 5 a.m. The beetles were found on the plant, not on the sides of their cage. On each occasion some were feeding with their rostrums sunk in the tissue.

Feeding holes could be found in almost any stem internode, and occasionally very small perforations were seen in the side branches. When newly made the holes could be detected by their small central opening and the surrounding area of lighter epidermis where the underlying tissues had been removed. In the laboratory these excavations frequently reached the opposite epidermis, while in stems brought in from the field they rarely went deeper than the central cylinder. The epidermis above the excavations turned brown within a few days and then became black, rather hard and brittle. Empty cavities in the apical internodes usually became dry and often contained fungi, while cavities in lower internodes were usually moist or even waterlogged.

On 10th July, a large patch of *Equisetum* at the University was cut down. This provided an opportunity to survey the feeding and oviposition scars. Four hundred and seventy-two scarred stalks were examined, of which 292 were found to contain only feeding holes. The number of stalks containing eggs was 151 (108 with one egg, 38 with two eggs, 3 with three eggs, 1 with four eggs, 1 with five eggs), and the number containing larvae was 29 (27 with one larva, 1 with two larvae, 1 with three larvae). In all 202 eggs and 32 larvae were found, 27 of the latter being in the first instar and three in the second.

Equisetum stems taken from the cage in the laboratory frequently contained up to 12 feeding holes and on one occasion 22 eggs were found in the one stem,

but in this case nine beetles had been confined with it for 48 hours. Occasionally six eggs were found in one hole. This is not necessarily due to overcrowding, as stalks containing four eggs in one hole were occasionally found in the field.

Copulation.

Copulations were frequently observed from 29th May until 18th August, both in the laboratory and in the open and must have occurred before 29th May as eggs were found on that date. They varied in duration from less than ten minutes to over an hour depending on the response of the female. An isolated pair of beetles was frequently seen in copulation, sometimes more than once a day. This does not necessarily mean that repeated matings are essential for maximum egg production. Unfortunately, it was not possible to determine whether the females taken from the field were virgin or not. The above-mentioned pair were isolated on 14th July, and egg laying ceased on 3rd August. During this time 27 eggs were laid.

A female isolated on 8th July laid an egg that day and continued laying until 5th August. Between 8th and 14th July 15 eggs were laid, while between 14th July and 5th August 26 eggs were laid, making a total of 41 eggs laid in isolation. This represents an average of one and a half eggs per day, almost the same rate as in the isolated pair, which suggests that the presence of the male had little influence on egg production.

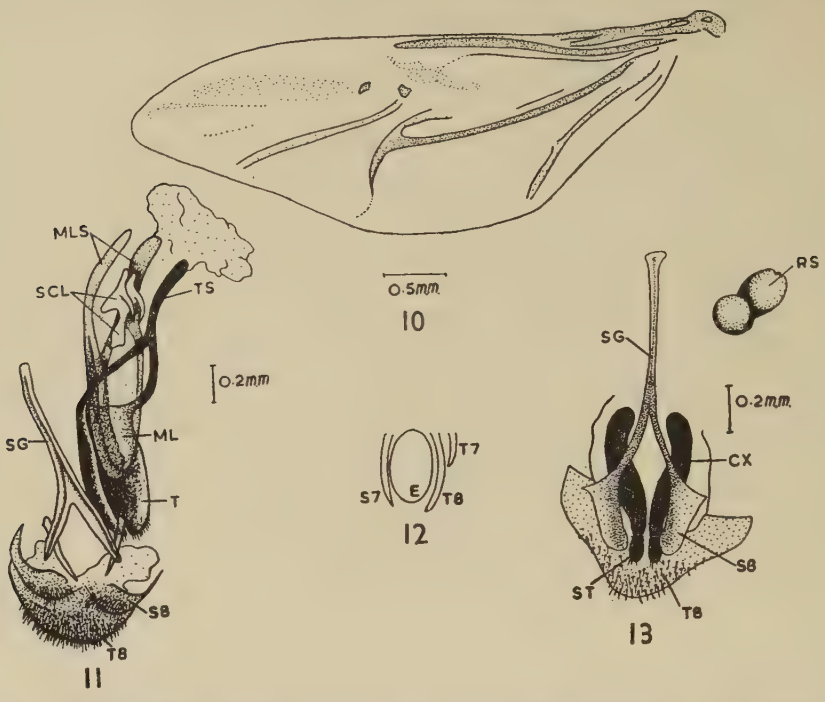
Oviposition.

Very occasionally eggs were laid on the cage or the surface of the plant. Normally the female excavated a hole with her rostrum in one of the internodes. As the rostrum sinks deeper into the tissue the antennae fold back into their scrobes. By straightening the hind legs the body is tilted forward so that the rostrum can reach the tissues below it. After feeding in this way for some time the rostrum is withdrawn, the weevil turns round and moves backwards until the tip of its abdomen is above the hole. It appears to feel the size and shape of the hole carefully, then exserts the ovipositor which forms a short thick tube over it. At first a yellow fluid seems to be secreted, then the tube dilates slightly and becomes opaque as the egg enters. The egg remains there for 2 or 3 seconds then slips rapidly into the hole below. A white, rather viscous fluid is then secreted over the hole. The trowel-shaped valve of the genitalia, tergite 8 (figs. 12 and 13, *T*8), scrapes the white fluid from the edges neatly over the hole, and dabs up and down as though to compact it. The white secretion solidifies very rapidly and when examined after the beetle has moved away it is found to have formed a hard crust and has not run into the hole. This crust was not invariably found over oviposition holes either in the laboratory or in the field.

Description of Eggs and Hatching.

The eggs vary considerably in shape, size and colour. Just after oviposition they are firm and cylindrical but, as the embryo develops, they lose the firm symmetrical outline. The average length was 2·0 mm., the

extreme limits 1·5–2·5 mm., but the majority varied little from the average. Breadth also varies, but to a lesser extent, the average being 0·56 mm.



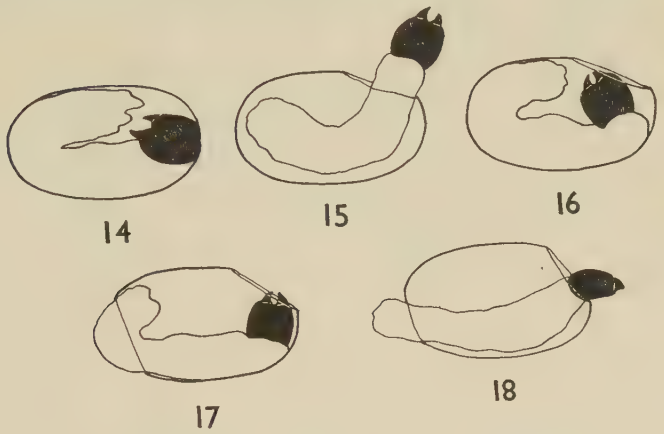
Figs. 10–13.—*Grypidius equiseti* F. (10) Wing. (11) Male genitalia. (12) Position of egg in ovipositor immediately prior to laying. (13) Female genitalia.

CX, coxa ; *E*, egg ; *ML*, median lobe ; *MLS*, median lobe strut ; *RS*, receptaculum seminalis ; *S*7, seventh sternite, *S*8, eighth sternite ; *SCL*, sclerotisations ; *SG*, spiculum gastrale ; *ST*, stylus ; *T*, tegmen ; *T*7, seventh tergite ; *T*8, eighth tergite ; *TS*, tegminal strut.

Colour varies from very pale yellow to quite a vivid orange. Frequently eggs brought in from the field were dark brown owing to an enveloping film of brown matter which could readily be scraped away to disclose a yellow or orange egg. As eggs without the brown cover invariably took longer to hatch than those with it, they must have been more recently laid and had not yet had sufficient time to acquire this brown covering. It is possible that the damaged tissues of the growing plant have some connection with its formation. Hatching usually takes place from 16 to 17 days after oviposition but, if several eggs have been laid in the one hole so that they are closely adpressed, hatching may not take place until the 21st or 22nd day.

On 23rd June an eclosion was observed through a binocular microscope. The position of the larva within the egg prior to hatching can be seen in figure 14. It alternately contracted and expanded the posterior part of the abdomen until the egg-bursters had torn a hole in the egg membrane. It wriggled round until it succeeded in getting its head out (fig. 15). In order to make these observations, part of the stem above the egg had been removed so that when the larva had reached the stage shown in figure 15 it failed to make any contact

with the plant and, presumably owing to this, retreated into the egg membrane (fig. 16). Again it contracted and expanded its abdomen until the egg capsule tore (fig. 17), and the abdomen was pushed out (fig. 18). The extruded tail portion made contact with the plant and the larva left its shell backwards. It then worked its way backwards along the central hollow of the *Equisetum* stem to the node above. In this case the stem had been held with its axis horizontal, instead of the normal vertical. Very occasionally a larval trace could be found starting up stem, but on reaching the node it would turn round



Figs. 14–18.—*Grypidius equiseti* F. Stages in hatching of the larva.

and travel back down the internode to the node below. It seemed to require the weight of its body above the mandibles to add sufficient force to penetrate the nodes, which are probably difficult to pass through because of the vascular strands passing out to the lateral branches.

In some places small excavations were visible in the parenchyma where the larva had taken a meal. Elsewhere it had moved straight down the central cylinder. Frass marks the route, the greatest accumulations being found just before each node, as though the larva had spent some time there.

Methods Used in Rearing Larvae.

Adults kept in the laboratory were given one or two fresh *Equisetum* stems each day. Some of the old stems containing eggs were dated and put in a jar with a little water at the bottom ; the eggs were removed from the others and kept in petri dishes on damp blotting paper where they took up less space and could be examined rapidly.

Newly hatched larvae were inserted into freshly gathered *Equisetum* stems by cutting back a flap of the plant tissue, placing the larva in the central cavity and replacing the flap. To prevent moisture escaping from the damaged area Vaseline was rubbed over it, or Cellotape applied. Larvae were usually removed and inserted into a fresh stem after about a fortnight and in this way could be reared as far as the third instar. After this stage they had to be transferred to a growing plant.

Description of Larvae and Development.

The terminology of Anderson (1947) is used.

Drawings were made with the assistance of a " Precision " microprojector (figs. 19–33). The head is free, the frons bearing five pairs of setae; *fs*4 and *fs*5 (fig. 22) are subequal and long, and there is a short endocarina. In older larvae there is a faint indication of ocelli.

Apart from the head, the only sclerotisation is a small dorsal area of the prothorax. The thoracic and pedal lobes each bear one, and the abdominal pleura two large setae. Bicameral spiracles are found on the prothorax and segments one to eight of the abdomen.

Newly hatched larvae are primrose-yellow, with long golden setae, and a pair of egg-bursters on each of the first six abdominal segments.

In their first instar they are very agile and readily climb glass surfaces. To move over smooth surfaces the head is held in position and the body contracted so that the posterior segments are drawn forwards. The terminal segment is now anchored and the head and the rest of the body moves forward. The movement is caused by waves of contraction and elongation, which are not separate but flow into each other so that the progression of the larva is smooth and undulating.

First instar larvae spent 12–16 days eating and travelling down stem. After moulting the second instar larvae continued down stem, then in a further 12–16 days moulted again. Third instar larvae spent the whole stadium in the stem, if this was large, or entered the rhizome. Fourth instar larvae were always found in the rhizome. That there were at least four instars I was able to ascertain by observing cast skins. An examination of head capsule measurements suggests that there may be five instars, the first three being well defined and the last two intergrading (Table I). Final instar larvae were found either

Table I.—*Measurement of head capsule (in millimetres).*

	Average.	Minimum.	Maximum.	Difference.	Number measured.
1st instar . . .	0·37	0·32	0·42	0·10	25
2nd instar . .	0·54	0·47	0·60	0·13	25
3rd instar . . .	0·73	0·68	0·77	0·09	9
4th or 4th + 5th instar	0·98	0·84	1·11	0·27	19
4th instar . . .	0·91	0·84	0·97	0·13	10
5th instar . . .	1·06	1·00	1·11	0·11	9

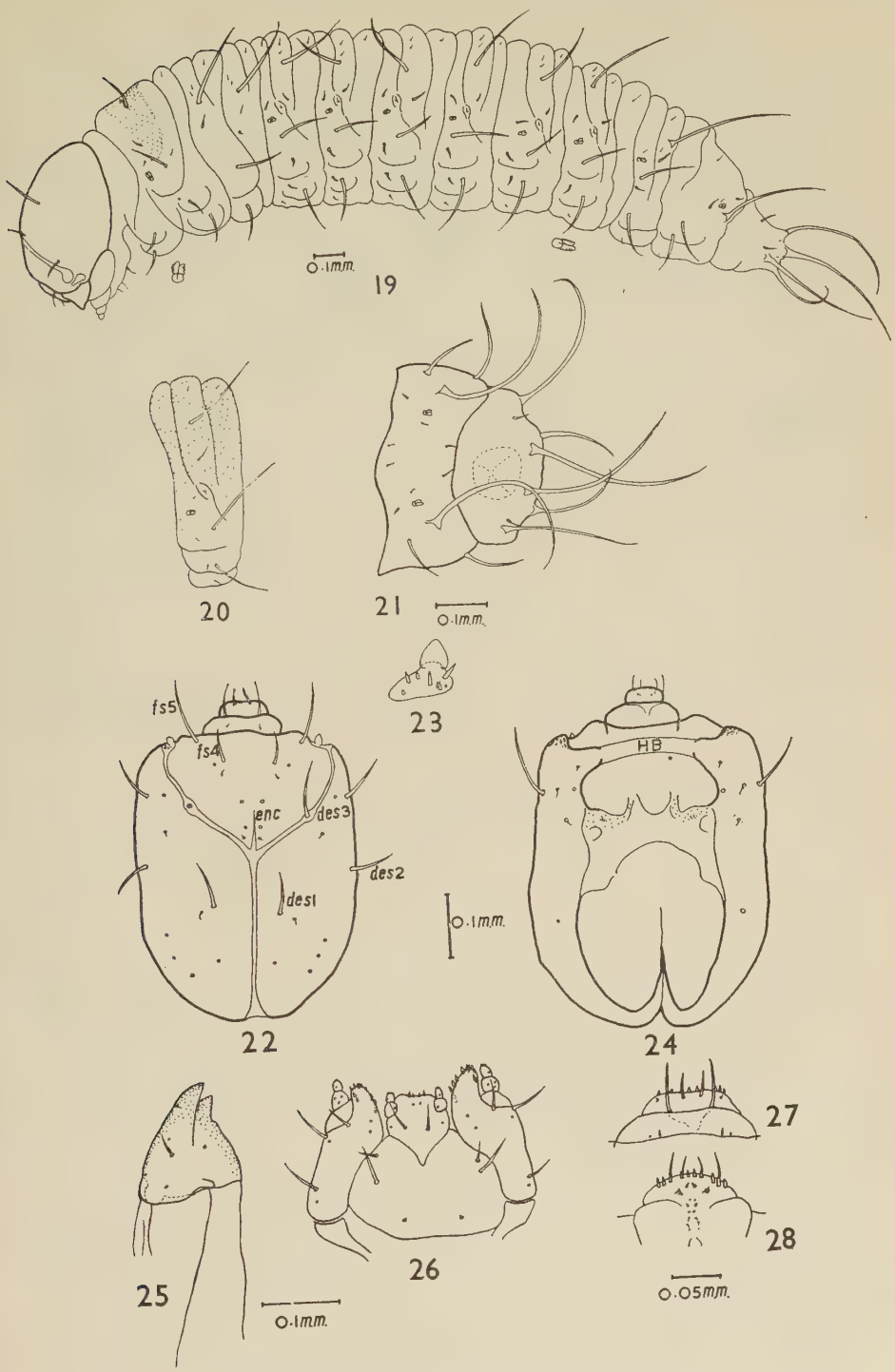
Ratio of head capsule widths.

$$\frac{0\cdot54}{0\cdot37} = 1\cdot46 \qquad \frac{0\cdot73}{0\cdot54} = 1\cdot35 \qquad \frac{0\cdot91}{0\cdot73} = 1\cdot25 \qquad \frac{1\cdot06}{0\cdot91} = 1\cdot16$$

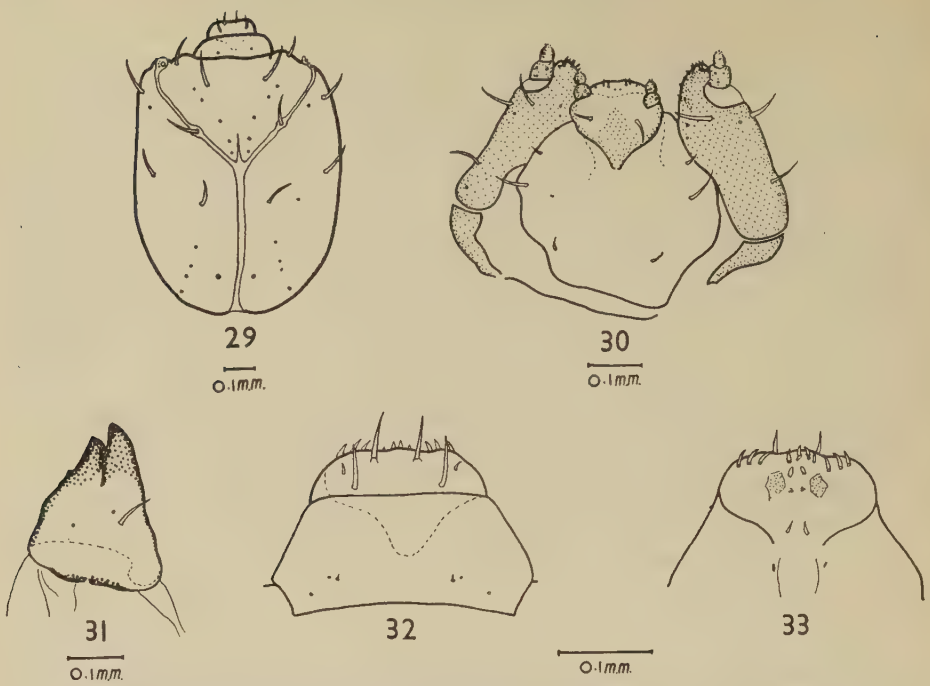
$$\frac{1\cdot46}{1\cdot35} = 1\cdot08 \qquad \frac{1\cdot35}{1\cdot25} = 1\cdot08 \qquad \frac{1\cdot25}{1\cdot16} = 1\cdot08$$

Figs. 19–28.—*Grypidius equiseti* F. (19) First instar larva. (20) An abdominal segment showing the sculpture. (21) Dorsal view of segments 8 and 9. (22) Dorsal view of head capsule. (23) Antenna. (24) Ventral view of head capsule. (25) Mandible. (26) Maxillae and labium. (27) Dorsal view of labrum. (28) Epipharynx.

des, dorsal epicranial seta; *enc*, endocarina; *fs*, frontal seta; *HB*, hypopharyngeal bracon.



FIGS. 19–28—(For explanation see facing page)



Figs. 29–33.—*Grypidius equiseti* F. (29) Head capsule of third instar larva. (30) Labium and maxillae. (31) Mandible. (32) Dorsal surface of labrum. (33) Epipharynx.

in the rhizome, when they were usually tightly encompassed by the plant, or curled up in the shells of the tubers, the starchy contents of which they had entirely consumed. Apparently winter is spent in the larval stage, since final instar larvae were still found in the rhizomes on 28th February and no pupae were found.

Discussion.

The first instar larvae of *Grypidius* possess what van Emden (1946) calls "persistent thoraco-abdominal egg-bursters", which he described in only four weevil larvae; *Calandra oryzae* has egg-bursters on abdominal segments four to six, *Deporaus betulae* on one to seven, *Attelabus nitens* on five and six, and *Calomycterus* sp. on segment eight. S. M. Hammad (1955) noted that *Pentarthrum huttoni* had three pairs of egg-bursters on abdominal segments one, two and three. *Grypidius* differs from all of these in having egg-bursters on abdominal segments one to six.

The number of larval instars varies from genus to genus in the Curculionidae, and there appears to be no constancy in the variation in width of the head capsule in each instar, nor in the amount of overlap of head capsule width with adjacent instars. O. W. Richards (1947) noted that *Calandra granaria* had four larval instars. In both *Calandra* and *Pentarthrum* there was a variation in the width of the head capsule in each instar but no overlap between adjacent ones. In one of Richards' *Calandra* cultures the mean width of the head capsule in the first instar was 0·24 mm. with a range of $\pm$ 0·02 mm., in the second

0·345 mm. ± 0·045 mm., in the third 0·515 mm. ± 0·055 mm. and in the fourth instar 0·68 mm. ± 0·06 mm. There is an irregular increase in the range in succeeding instars.

Using Dyar's law, S. M. Hammad (*l.c.*) deduced that *Pentarthrum huttoni* had five larval instars. According to him the variation in the width of the head capsule in all five instars is 0·04 mm. ; the mean width of the head capsule in the first instar is 0·22 mm. and in the fifth instar 0·61 mm.

In *Cleonus piger* Scop. there appear to be four instars, the head sizes of which do not overlap in adjacent instars, and there is an increasing variation in their widths in succeeding instars. In *Zacladus geranii* Payk. only the first instar is distinct ; the others intergrade.

In *Grypidius equiseti* the range in the head capsule width in the first instar was 0·10 mm., in the second 0·13 mm., in the third 0·09 mm. (nine only were measured ; if a larger number had been available the range would probably have been slightly greater) and in the succeeding instar or instars (it may be the fourth or the fourth and fifth) 0·27 mm. The range is fairly constant in the first three instars and then more than doubles. This may indicate that this last instar is composed of two intergrading ones. If this hypothesis is adopted, it is found that the increase of the head capsule widths, from instar to instar, decreases by a constant factor of 1·08 (Table I).

It seems probable that the quality and quantity of food available to the larva may to a small extent affect the width of its head capsule at the moult. Up to their third instar *Grypidius* larvae are unlikely to be affected by the condition of the host plant, so that the head width is unlikely to vary much from the optimum. After this stage they require much more food and the size and succulency of the rhizome may well affect the head width at the moult.

Summary.

Recorded food plants for *Grypidius equiseti* are *Equisetum arvense* and *E. palustre*. The only species of *Equisetum* occurring near Glasgow on which it would feed or oviposit readily was *E. arvense*, which was also the only species on which it was found in the field.

I found no evidence that *G. equiseti*, found in the Glasgow area, were able to fly. Despite this, and the fact that it appears to be confined to two species of *Equisetum*, it has a fairly widespread distribution.

Observations were made on thanatosis in this species.

The period of copulation and oviposition is extended.

The female uses her rostrum to excavate a cavity in the *Equisetum* stem in which the eggs are laid. Egg-bursters and mandibles assist the larva to break out of the egg membrane, which the larva does not consume.

There are either four or five instars, the first and second being from 12 to 16, and the third from 12 to 20 days' duration. First and second instars, usually the third and occasionally part of the fourth, are spent travelling down the stem ; fully grown larvae are always found in the rhizome or tubers. The winter is passed as a final instar larva, pupation presumably occurring in early spring. The adults emerge in April and May.

The adult anatomy does not appear to differ greatly from other Curculionids studied. The sex ratio appears to be even.

Acknowledgments

This work was carried out while I was in receipt of a grant from the Department of Scientific and Industrial Research. I wish to thank Mr. R. A. Crowson for the great assistance he has given me throughout. I would also like to thank Dr. F. I. van Emden for his advice on the measurement of larval head-capsules, Dr. W. H. Anderson for bringing the ocelli of the larvae to my attention, and Dr. J. W. H. Lawson for a number of helpful suggestions.

References.

Anderson, W. H., 1947, A terminology for the anatomical characters useful in the taxonomy of weevil larvae. *Proc. ent. Soc. Wash.* **49** : 123–32.

Bargagli, P., 1884, Rassegna biologica di rincofori Europei. *Bull. Soc. ent. Ital.* **16** : 149–287.

Emden, F. I. van, 1946, Egg-bursters in some more families of polyphagous beetles and some general remarks on egg-bursters. *Proc. R. ent. Soc. Lond.* (A) **21** : 89–97.

Fabre, J. H., 1918, *The glow-worm and other beetles.* Translated by A. T. de Mattos. London.

Fowler, 1891, *The Coleoptera of the British Isles*, **5**. London.

Hammad, S. M., 1955, The immature stages of *Pentarthrum huttoni* Woll. *Proc. R. ent. Soc. Lond.* (A) **30** : 1–3.

Hustache, A., 1930, Curculionidae Gallo-Rhénans. *Ann. Soc. ent. Fr.* **99** : 81–272.

Jackson, D. J., 1933, Observations on flight muscles of *Sitona* weevils. *Ann. appl. Biol.* **20** : 731–70.

Richards, O. W., 1947, Observations on the grain weevil, *Calandra*. *Proc. zool. Soc. Lond.* **117** : 1–43.

THE SPERMATHECA AS A TAXONOMIC CHARACTER IN ACRIDOIDEA (ORTHOPTERA).

By V. M. Dirsh.

(*Anti-Locust Research Centre*).

In a series of papers, Slifer (1939–43) described the internal female genitalia, mainly the spermatheca, in Acridoidea and suggested that the spermatheca may provide additional taxonomic characters for this group of insects. Voy (1949) studied the whole of the female genitalia in the main groups of Orthopteroids and concluded that the spermatheca is very characteristic for each suborder and even each family. Recently, the system of Acridoidea was rearranged, mainly on the basis of male genitalia (Dirsh, 1956); this is now followed by a review of spermathecae in all families, based on Slifer's data as well as, in the case of previously unstudied and recently erected families, my own observations.

Since dry specimens were used, it was not always possible to extract the fragile spermathecal duct; in such cases only the spermatheca is figured.

Family Eumastacidae.

The spermatheca is simple, sac-like, globular or inversely pear-shaped, with a thin and comparatively short spermathecal duct.

Family Tanaoceridae.

The spermatheca of this remarkable family remains unstudied.

Family Pneumoridae. (Figs. 1–4).

The spermathecae of four genera were studied by me: *Physemacris* Roberts, 1941; *Bullacris* Roberts, 1941; *Pneumora* Thunberg, 1775; *Shortridgea* Peringuey, 1916. By the shape of the spermatheca the family is sharply divided into two groups: to the first belong *Physemacris* and *Bullacris*, which possess a vermicular spermatheca with three or four vermicular diverticula (figs. 1, 2). In the second group, consisting of the genera *Pneumora* and *Shortridgea*, the spermatheca is a large sac-like reservoir with three or four large pocket-like diverticula (figs. 3, 4).

It is worthy of note that the male epiphallus shows the same striking diversity between these two groups of genera as the spermatheca (Dirsh, 1956).

Family Xyronotidae.

The spermatheca is simple, elongated and slightly curved, with a single apical diverticulum (Slifer, 1943).

Family Trigonopterygidae. (Fig. 5).

The genera *Systella* Westwood, 1841, and *Trigonopteryx* Charpentier, 1841, studied by me, have an identically shaped spermatheca, which is simple and elongated, with a single, strongly curved, apical diverticulum. It merges

gradually into a long spirally coiled spermathecal duct, which is very narrow near the spermatheca and widens gradually towards the proximal end.

Family Proscopiidae.

In the only genus, *Cephalocoema* Serville, 1839, studied by Slifer (1943), the spermatheca is tube-like, elongated, with a broad apical diverticulum and with two additional vermicular diverticula at its base. The spermathecal duct is short and very broad.

Family Charilaidae. (Fig. 6).

In the genus *Charilaus* Stål, 1875, studied by me, the spermatheca is elongated, with a curved apical diverticulum and a small preapical one. The spermathecal duct is narrow, but widens in the last fourth of the proximal end.

Family Pamphagidae.

The spermatheca has a single elongated, more or less curved, diverticulum, which sometimes forms several lateral bulges (Slifer, 1940).

Family Pyrgomorphidae.

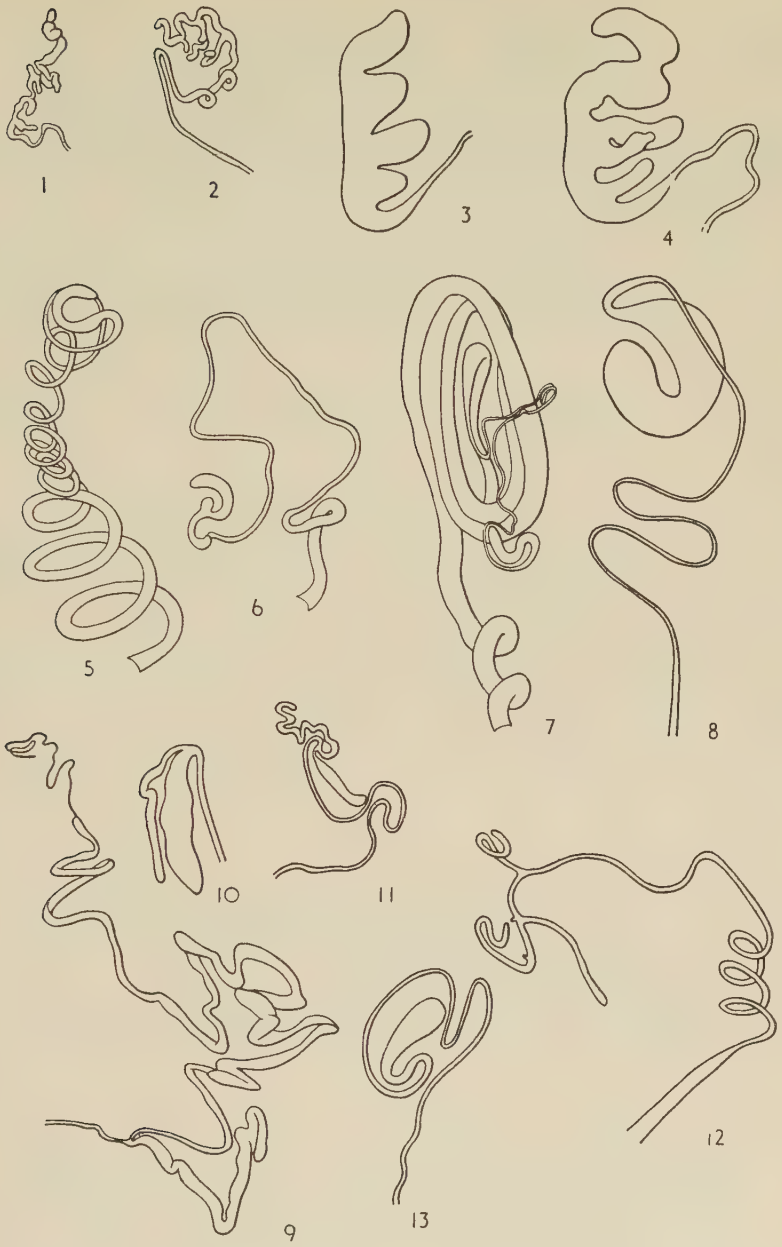
In this family, the spermatheca is represented by several forms : (1) simple, elongated, more or less curved, with a single apical diverticulum ; (2) elongated, vermicular, strongly and irregularly curved ; (3) with an apical diverticulum and a small or large preapical one ; (4) with one apical and numerous long vermicular additional diverticula (Slifer, 1940, 1943).

Family Lentulidae. (Figs. 7–26).

The following genera of this recently erected family were studied by me : *Lentula* Stål, 1878 ; *Paralentula* Rehn, 1944 ; *Sygrus* I. Bolivar, 1889 ; *Mecostibus* Karsh, 1896 ; *Rehnula* Uvarov, 1939 ; *Devylderia* Sjöstedt, 1923 ; *Swaziacris* Dirsh, 1953 ; *Basutacris* Dirsh, 1953 ; *Eremidium* Karsch, 1896 ; *Gymnidium* Karsch, 1896 ; *Betiscoides* Sjöstedt, 1923 ; *Lithidium* Uvarov, 1925 ; *Eneremius* Saussure, 1888.

The spermathecae in this family vary in structure. Those of the first group are characterised by a single, simple, curved apical diverticulum (*Lentula*, fig. 7 ; *Rehnula*, fig. 8 ; *Eremidium*, fig. 13 ; *Sygrus*, figs. 14, 15 ; *Gymnidium*, fig. 19 ; *Lithidium*, fig. 22 ; *Paralentula*, figs. 23, 24 ; *Betiscoides*, fig. 26). In all of them there is a gradual narrowing to the narrow spermathecal duct, which is strongly widened in its proximal part. The whole spermathecal duct in normal position is spirally coiled or is folded in its proximal widened part, so that both halves are parallel (figs. 19, 26).

The second group differs in the shape of the spermathecae, which possess the apical and preapical diverticula (*Mecostibus*, figs. 9, 10 ; *Devylderia*, fig. 11 ; *Basutacris*, figs. 16, 17 ; *Eneremius*, figs. 20, 21). Some of them, besides a preapical diverticulum, have also one or two additional ones (figs. 9, 17). The spermathecal duct in this group is similar in its shape to that of the first group. It is necessary to note that the spermatheca of *Eneremius* (fig. 21) is suspiciously like that of the subfamily Acridinae ; the position of this genus is uncertain, since males are still unknown.



FIGS. 1–13.—(1–4) Fam. Pneumoridae: (1) *Physemacris variolosa* (Linné, 1758); (2) *Bullacris longicornis* (Stål, 1873); (3) *Pneumora inanis* (Fabricius, 1775); (4) *Shortridgea absidata* (Karsch, 1896). (5) Fam. Trigonopterygidae: *Systella rafflesii* Westwood, 1841. (6) Fam. Charilaidae: *Charilaus carinatus* Stål, 1875. (7–13) Fam. Lentulidae: (7) *Lentula obtusifrons* Stål, 1878; (8) *Rehnula usambarica* (Ramme, 1929); (9) (10) *Mecostibus minor* (Bruner, 1910); (11) *Devylderia capensis* Dirsh, 1956; (12) *Swaziacris burtti* Dirsh, 1953; (13) *Eremidium obtusus* Dirsh, 1956.

The third group is characterised by a branching spermatheca (*Swaziacris*, fig. 12).

Family Lathiceridae. (Fig. 27).

In the genus *Lathicerus* Saussure, 1888, studied by me, the spermatheca is simple, elongated and strongly curved with a single diverticulum, but with a tendency to form a preapical one.

Family Ommexechidae.

The spermatheca is large, elongated and sac-like, with a diverticulum at its distal end or in the middle. The diverticulum has two or three small secondary ones (Slifer, 1940).

Family Pauliniidae.

The spermatheca bears an apical and a small preapical diverticula (Slifer, 1939).

Family Acrididae.

This family is now divided into the following subfamilies: Romaleinae, Catantopinae (Cyrtacanthacridinae of some authors), Calliptaminae, Eurypyminae, Hemiacridinae, Acridinae (which include former Oedipodinae as a tribe), Egnatiinae, Eremogryllinae and Truxalinae (see Dirsh, 1956).

The spermatheca is uniform throughout the whole family (with some exceptions, *see below*). It has an apical diverticulum and a more or less developed preapical one (Slifer, 1939, 1943) of different relative size and shape, sometimes with one or more additional, mainly short, secondary ones.

The characteristic features of the spermatheca of the different subfamilies are as follows:

Subfamily Romaleinae.

The typical spermatheca for the subfamily has a large, elongated, mostly vermicular, apical diverticulum. The preapical diverticulum is very small, rudimentary, or disappears completely (gen. *Tytthotyle* Scudder, 1897) (Slifer, 1940, figs. 5–16; 1940*a*, fig. 8; 1943, fig. 2).

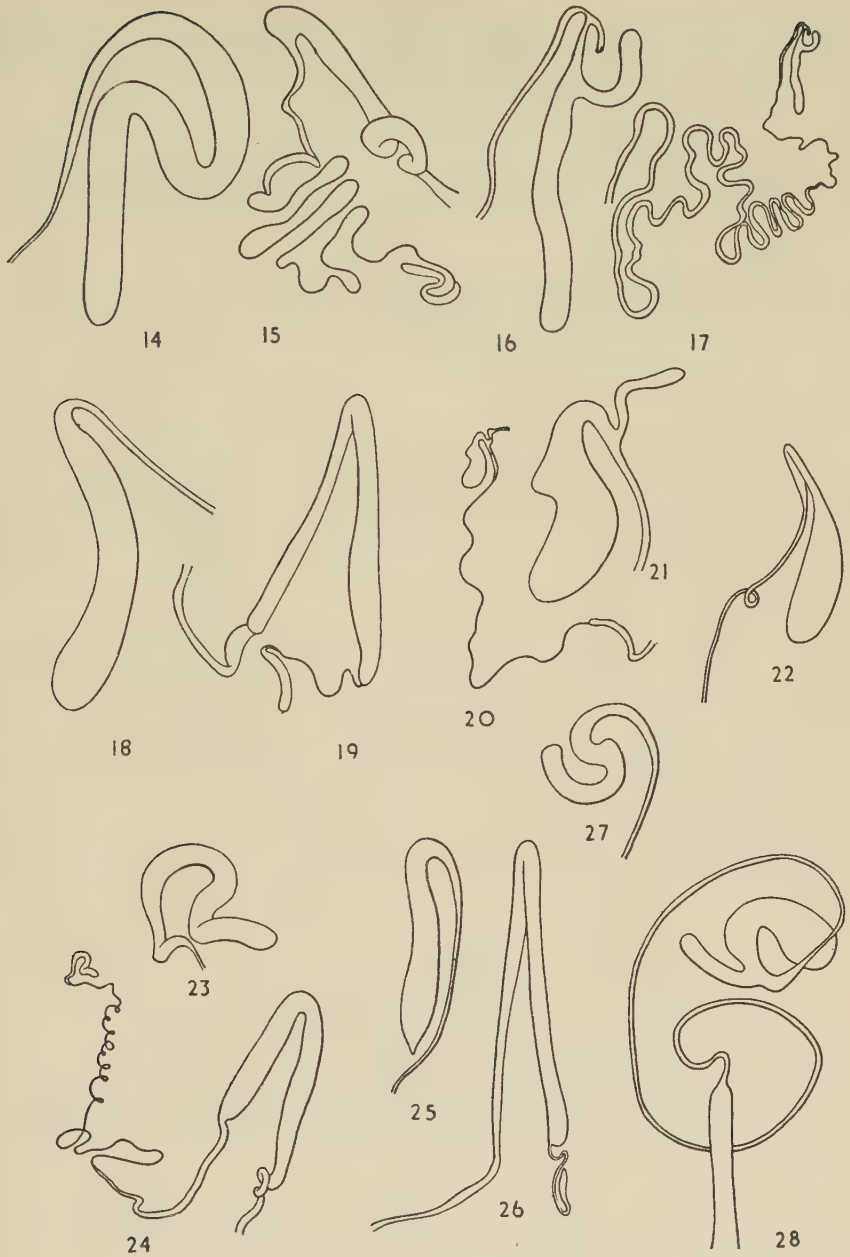
In two Old World genera of this subfamily, *Kabulia* and *Teratodes*, the preapical diverticulum is large, and there are one or several secondary ones (Slifer, 1940*a*, figs. 61, 112).

Subfamily Catantopinae.

The spermatheca in this subfamily has apical and preapical diverticula, both varying from short finger-like to long vermicular processes, which in the last case sometimes widen to a sac-like shape. Sometimes an additional diverticulum and secondary ones occur, but on the whole the structure is rather uniform in the subfamily (Slifer, 1940*a*).

Subfamily Calliptaminae.

The spermatheca has apical and preapical diverticula, both short or moderately long. On the whole, it does not differ in principle from that in the previous subfamily (Slifer, 1940*a*).



FIGS. 14–28.—(14–26) Fam. Lentulidae: (14) (15) *Sygrus rehni* Dirsh, 1956. (16) (17) *Basutacris scotti* Dirsh, 1953. (18) (19) *Gymnidium turbinatum* Karsch, 1896. (20) (21) *Eneremius namaquensis* Dirsh, 1956. (22) *Lithidium pusillum* Uvarov, 1925. (23) (24) *Paralentula candidoi* (Ramme, 1929). (25) (26) *Betiscoides meridionalis* Sjöstedt, 1923. (27) Fam. Lathiceridae: *Lathicerus cimex* Saussure, 1888. (28) Fam. Acrididae, Subfam. Eremogryllinae: *Eremogryllus hammadae* Krauss, 1902.

Subfamily Euryphyminae.

The spermatheca has apical and preapical diverticula and does not differ from that in Catantopinae and Calliptaminae (Slifer, 1940*a*).

Subfamily Hemiacridinae.

The spermatheca has apical and preapical diverticula, the apical one comparatively long; it does not deviate from that of other subfamilies of Acrididae.

Subfamily Acridinae.

The spermatheca has apical and preapical diverticula; the apical one is usually comparatively short and sometimes has small secondary diverticula; the preapical one is usually sac-like (Slifer, 1939).

Subfamily Egnatiinae.

This subfamily has a single re-curved, sac-like diverticulum (*Egnatioides*, *Charora*) or a very short apical diverticulum and a sac-like preapical one (*Egnatius*). Where the diverticulum is single its position and shape suggest that it is the preapical one, the apical one being lost (Slifer, 1939).

Subfamily Eremogryllinae. (Fig. 28).

The two genera constituting this subfamily, *Eremogryllus* Krauss, 1902 and *Notopleura* Krauss, 1902, were studied by me. In both the spermatheca has finger-shaped apical and sac-like preapical diverticula, and it does not differ from the spermatheca of Acridinae and Truxalinae. In the shape of epiphallus, however, Eremogryllinae are very different from these subfamilies (Dirsh, 1956).

Subfamily Truxalinae.

The spermatheca has apical and preapical diverticula and is similar to that in Acridinae (Slifer, 1939).

Discussion.

The spermatheca in Acridoidea presents five main types:

(1) A single, globular or pear-shaped reservoir, which is not twisted sideways or backwards. This type occurs in Eumastacidae only.

(2) The second type of spermatheca is one with a single elongated and mostly S-curved diverticulum. This type is found in Xyronotidae, Trigonopterygidae, Pamphagidae, some Pyrgomorphidae, some Lentulidae and in Lathiceridae.

(3) The third type is a sac-like spermatheca with pocket-like bulges on one side. This type was found only in the genera *Pneumora* and *Shortridgea* of Pneumoridae.

(4) The fourth type has apical and preapical diverticula, sometimes with a secondary diverticulum or diverticula and rarely with an additional one. This structure is usual for the whole family Acrididae, with the exception of the subfamilies Romaleinae and Egnatiinae, in which one of the diverticula is reduced or absent.

(5) The fifth type is a branching spermatheca with several vermicular or finger-shaped diverticula arising at different points of the main stem or rarely radiating from one point in all directions. This type occurs in the genera *Physemacris* (fig. 1) and *Bullacris* (fig. 2) of Pneumoridae and in some genera of Pyrgomorphidae and of Lentulidae (fig. 12).

The distribution of the types of spermatheca is given in the table.

TABLE I.—*Distribution of types of spermatheca in families of Acridoidea.* (*Explanation in text*).

Families.	Type of spermatheca. 1.	2.	3.	4.	5.
Eumastacidae	×	.	.	.	.
Tanaoceridae	?	?	?	?	?
Pneumoridae	.	.	×	.	×
Xyronotidae	.	×	.	.	.
Trigonopterygidae	.	×	.	.	.
Proscopiidae	.	.	.	.	×
Charilaidae	.	.	.	×	.
Pamphagidae	.	×	.	.	.
Pyrgomorphidae	.	×	.	×	×
Lentulidae	.	×	.	×	×
Lathiceridae	.	×	.	.	.
Ommexechidae	.	.	.	.	×
Pauliniidae	.	.	.	×	.
Acrididae	.	.	.	×	.

These five main types of spermatheca are not clearly separable and all intermediate forms can be found (*see* figures in Slifer, 1939–43 and in this paper). Nevertheless, there are families and even subfamilies or groups of genera which have fairly uniform and characteristic spermathecae. As an example of generic groups, the two in Pneumoridae (figs. 1, 2, 3 and 4) may be quoted. The largest family, the Acrididae, is rather uniform if one excludes Romaleinae. The New World Romaleinae have a uniform but different spermatheca, with one of the diverticula reduced and almost disappearing. This suggests that the subfamily might probably be ranked as a family.

In the Pamphagidae the spermathecae are also rather uniform. In contrast, in the Pyrgomorphidae, a family which is very compact and well defined by the external characters and by the male phallic complex (Dirsh, 1956), the spermathecae are extremely diverse and all types except the first and the third are found.

In the smaller families consisting of few genera, the spermathecae are in all cases uniform.

The question is whether the structure of the spermatheca is correlated with the external characters and with the male phallic complex in the subdivisions of Acridoidea. Although in Pamphagidae the external features and the phallic complex are very uniform and characteristic and the spermatheca is uniform as well, the same type of spermatheca occurs also in Xyronotidae, Trigonopterygidae, Pyrgomorphidae, Lentulidae and Lathiceridae.

In the case of Pyrgomorphidae, which also have very good external charac-

ters and a uniform and very characteristic phallic complex, the spermathecae are extremely diverse (see Table).

In Lentulidae, in which the phallic complex is uniform, the external characters and the spermathecae are very variable.

In Acrididae, which have rather divergent external characters which, with those of the epiphallus (Dirsh, 1956), form the basis of the division into subfamilies, the spermathecae are relatively uniform.

All this indicates that the structure of the spermatheca cannot be used as a single taxonomic character, but sometimes it may be useful as an auxiliary one, though it must be used with due caution.

It is logical to suppose that the simplest pear-shaped or globular spermatheca of the Eumastacidae is the primitive one from which all other types have been derived. A support for this conclusion is lent by the fact that an almost identical type of spermatheca is found in Mantodea, Tettigonioidea and Gryllodea (Voy, 1949). Against this supposition, however, is the fact that the spermatheca in Blattodea (Voy, 1949) has apical and preapical diverticula and is generally similar to the Acridoid type which appears more advanced.

It must be emphasised, however, that only very few Mantodea, Tettigonioidea, Gryllodea and Blattodea were studied in this respect and the Acridoidea also need further study.

References.

Dirsh, V. M., 1956, The phallic complex in Acridoidea (Orthoptera) in relation to taxonomy. *Trans. R. ent. Soc. Lond.* **108** : 223–356, 66 plates.

Slifer, E. H., 1939, The internal genitalia of female Acridinae, Oedipodinae and Pauliniinae (Orthoptera, Acrididae). *J. Morph.* **65** : 437–55, 7 plates.

—— 1940, The internal genitalia of female Trinchinae, Batrachotetriginae, Pamphaginae and Pyrgomorphinae (Orthoptera, Acrididae). *Ibid.* **66** : 175–85, 5 plates.

—— 1940*a*, The internal genitalia of female Ommexechinae and Cyrtacanthacridinae (Orthoptera, Acrididae). *Ibid.* **67** : 199–216, 12 plates.

—— 1943, The internal genitalia of some previously unstudied species of female Acrididae (Orthoptera). *Ibid.* **72** : 225–31, 3 plates.

—— 1943*a*, The internal genitalia of female Tetrigidae, Eumastacidae and Proscopiidae (Orthoptera). *Ibid.* **73** : 89–97, 2 plates.

Voy, A., 1949, Contribution a l'étude anatomique et histologique des organes accessoires de l'appareil génital femelle chez quelques espèces d'orthoptéroides. *Ann. Sci. nat., Zool.* **11** : 270–345, 2 plates.

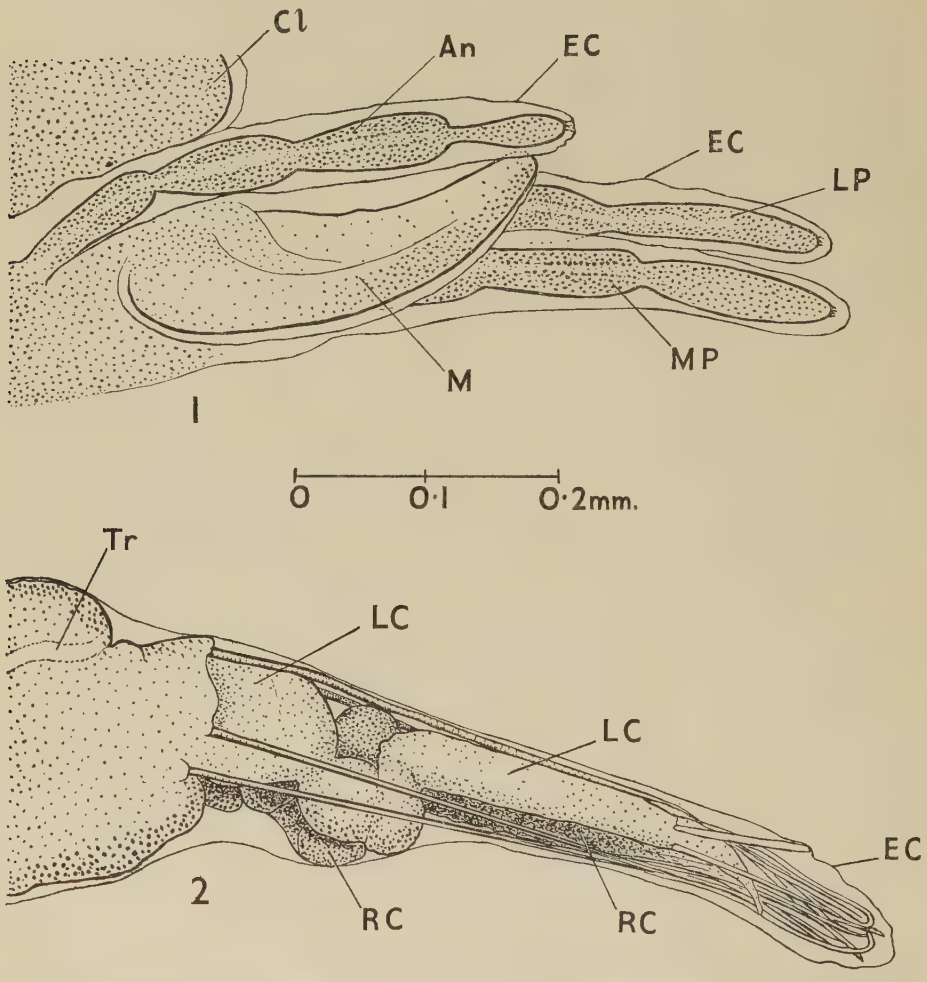
A NOTE ON THE EMBRYONIC CUTICLE SHED ON HATCHING BY THE LARVAE OF *AGABUS BIPUSTULATUS* L. AND *DYTISCUS MARGINALIS* L. (COLEOPTERA : DYTISCIDAE).

By Dorothy J. Jackson.

While watching the hatching of the eggs of *Agabus bipustulatus* L. I noticed that the larva always emerged from the egg with a delicate membrane surrounding its posterior segments or entangled on its legs or cerci. It was a uniform and very thin membrane, produced into various slender appendages. Some eggs with larvae about to hatch were mounted in an excavated slide in water. Under such conditions development is slowed up, perhaps because of an insufficiency of dissolved oxygen in the water. Several larvae hatched successfully, but others became immobile when only half emerged from the egg. In such specimens the whole of the exposed part of the body was seen to be surrounded with a fine cuticle which flattened the bristles against the body and enclosed each of the oral appendages, the antennae and the legs in a separate unsegmented bag of cuticle. On investigating eggs containing embryo larvae in earlier stages of development this embryonic cuticle showed more clearly (fig. 1), as it fitted loosely around the various appendages. Later, when the larva is nearly ready to hatch, the legs, antennae and mouthparts have increased greatly in size, so that they fill the embryonic cuticle tightly and are creased into numerous wrinkles. On pricking an egg containing a young embryo larva under water, the larva, being under pressure, may be expelled undamaged through the hole with the embryonic cuticle intact around it. This cuticle has no bristles and shows no segmental divisions. Posteriorly it terminates in a single tapering bag which encloses both cerci. At first the cerci extend straight within the cuticular covering but, as their growth proceeds, they become convoluted basally, so that in the larva before hatching the two groups of long bristles (three proximal and four subterminal on each cercus) lie near together and, owing to the curved position of the developing larva, they rest against the side of the neck, curiously enough always on the right side. The bristles of the cerci develop within this elongated bag of embryonic cuticle (fig. 2). All the other appendages, even the tarsal claws, are enclosed in individual sacs. The embryonic cuticle surrounds the head of the embryo larva and covers the egg-bursters.

In *Agabus bipustulatus* the egg-bursters consist of two spines, one on each side of the frons. They are conspicuous in the larva just before hatching as they are then black, set in a darkly pigmented spot, while the head is yellowish-white with red ocelli. The egg-bursters are a part of the first larval cuticle and so persist to the end of the instar, but after the head darkens in the emerged larva they are less noticeable. In the larvae that had emerged only half-way from the egg, the embryonic cuticle still surrounded the head, but whether it still covered the egg-bursters was not easy to determine as they did not show in profile. However, it seems probable that, had the spines pierced the cuticle, this, being very taut, would have split and slipped backwards, and, in one instance, when I moved a half-emerged larva so that the

spine of one side appeared in profile, the embryonic cuticle could be seen covering the spine completely. In these eggs with partially emerged larvae, the egg shell, consisting of chorion and vitelline membrane, had been ruptured in the usual manner, and it would appear that on these occasions the egg-bursters had not come into action. The conditions, however, were not normal (mounted in an excavated slide) but under more natural conditions—as in a dish of water—hatching is instantaneous. It is effected by the larva suddenly



Figs. 1–2.—*Agabus bipustulatus* L. (1) Lateral view of antenna and mouthparts of right side of embryo larva viewed through the transparent egg shell to show the embryonic cuticle surrounding each appendage. (The parts are all transparent, but to avoid confusion the underlying parts of the palps have been omitted). (2) Lateral view of posterior extremity of the body of an older embryo larva, removed from egg, showing the cerci with their bristles still enclosed by the embryonic cuticle. (Same scale as fig. 1).

An, antenna; *Cl*, clypeus; *EC*, embryonic cuticle; *LC*, left cercus; *LP*, labial palp; *M*, mandible; *MP*, maxillary palp; *RC*, right cercus; *Tr*, longitudinal tracheal trunk.

raising its head from the bent position when the egg shell splits open with a longitudinal rent down the front, the slit extending from the anterior pole of the egg nearly to the posterior end. Owing to the speed of the action I have so far failed to ascertain if the egg bursters effect the split. An account of the behaviour of the larva prior to hatching and a discussion of the probable action of the egg-bursters will be given in a later paper.

I have found that an embryonic cuticle occurs also in *Dytiscus marginalis* L., investing the embryo in just the same manner as in *Agabus bipustulatus*, except that the sacs enclosing the legs each show only a short terminal bifurcation for the tarsal claws. The egg-bursters, also situated on the frons, are similarly covered by this cuticle. In the hatched *Dytiscus* eggs which I have examined, the embryonic cuticle was not withdrawn from the egg, but was left protruding from the rent made by the larva in hatching. This hole is confined in *Dytiscus* to the anterior pole of the egg, and the aperture is small compared with the longitudinal slit left in the *Agabus* egg. This will account for the fact that the embryonic cuticle is largely retained within the *Dytiscus* egg after hatching, while in *Agabus bipustulatus* I have always observed that it is brought out of the egg by the larva.

As far as I am aware an embryonic cuticle has not been recorded before in the Dytiscidae, for Blunck (1914), in his detailed account of the embryo of *Dytiscus* and of the hatching of the larva, makes no mention of it, nor does he allude to it in his paper on *Agabus bipustulatus* (Blunck, 1921). An embryonic cuticle such as I have found in *Agabus* and *Dytiscus* has been recorded by Sikes and Wigglesworth (1931) in *Tenebrio molitor* L., and these authors observed that the cuticle was shed shortly before, or at the time of, rupturing the chorion. An embryonic cuticle, cast off at the time of hatching, has also been observed by Wheeler (1889) in *Doryphora* (*Leptinotarsa*) *decemlineata*, and this author states that Graber has made a similar observation on the embryo *Lina* (*Melasoma*). Weber (1954 : 21) states that an embryonic cuticle occurs in the Hemimetabola and is absent in most Holometabola, but occurs in *Sialis*, *Tenebrio* and Silphidae. The cuticle is secreted by the epidermis of the young embryo and Weber (1933 : 556) considers that it is comparable to a first larval skin. Since it is unsegmented it seems preferable to regard it as a provisional or embryonic cuticle (Wigglesworth, 1950).

In *Silpha obscura* and *Phosphuga atrata*, Verhoeff (1919) described an embryonic cuticle bearing hatching spines on the hypopharynx, but in *Agabus* and in *Dytiscus* the egg-bursters occur on the cuticle of the first instar larva being, as van Emden (1925) described, " persistent acral egg-bursters ". In a later paper (1946) van Emden describes egg-bursters in *Tenebrio molitor* in the form of minute tooth-like spines situated at the base of certain tall setae on both thoracic and abdominal segments. Since they occur on the cuticle of the first instar larva he terms them persistent thoraco-abdominal egg-bursters. He considers that in hemimetabolous insects and Neuroptera, etc., the embryonal cuticle shed immediately after hatching must be homologous with the first larval skin of the higher holometabolous insects. However, in view of the occurrence of an embryonic cuticle in a Tenebrionid, a Chrysomelid, and, as now recorded, in two Dytiscidae, it seems very probable that it will occur also in the eggs of other beetles. The embryonic cuticle in these Coleoptera would, therefore, appear to be homologous with that of the Hemi-

metabola and certain Holometabola, though it differs in not bearing the egg-bursters. Dr. van Emden informs me that he has not looked for an additional membrane during the hatching process, and it would be interesting to know if an embryonic cuticle is present in the eggs of Carabidae and other beetles. Since the egg of *Agabus* is transparent, this cuticle is quite easily seen when the egg is examined with a compound microscope by transmitted light; moreover, if the larva hatches in a small dish of clean water the discarded cuticle is evident. In the *Dytiscus* egg this cuticle is not quite so readily seen as in *Agabus*, partly on account of the greater opacity of the embryo and partly because the legs and appendages lie so close to the body. In the eggs of other beetles the cuticle may have been overlooked owing to the opacity of the egg shell, and, if the larvae hatched on soil or amongst vegetable matter and the cuticle was deposited outside the egg, it would not be so easily noticed, unless hatching were actually observed. Again it may be left within the egg, for this occurs in *Dytiscus*, and Sikes and Wigglesworth record that it may be shed in *Tenebrio* before the chorion is ruptured. Whether or not the presence of this inner cuticle interferes with the action attributed to the various "hatching" spines remains to be investigated.

Summary.

In *Agabus bipustulatus* L. an embryonic cuticle surrounds the embryo and encloses the antennae, mouthparts and legs in separate unsegmented sheaths. It covers the egg-bursters which are situated on the frons and are a part of the larval cuticle. This embryonic cuticle is shed by the larva on hatching. In *Dytiscus marginalis* L. a similar embryonic cuticle occurs, but it is largely retained within the egg on hatching. Though not bearing the egg-bursters, this cuticle appears to be homologous with the embryonic cuticle of the Hemimetabola and certain Holometabola.

References.

Blunck, H., 1914, Die Entwicklung des *Dytiscus marginalis* L. vom Ei bis zur Imago. I. Das Embryonalleben. *Z. wiss. Zool.* **3** : 76–151.

—— 1921, Kleine Beiträge zur Kenntnis des Geschlechtslebens und der Metamorphose der Dytisciden. 3. *Agabus bipustulatus* L. *Ent. Blätt.* **17** : 184–94.

Sikes, E. K. and Wigglesworth, V. B., 1931, The hatching of insects from the egg, and the appearance of air in the tracheal system. *Quart. J. micr. Sci.* **74** : 165–92.

van Emden, F. I., 1925, Zur Kenntnis der Eizähne der Arthropoden, inbesondere der Coleopteren. *Z. wiss. Zool.* **126** : 622–54.

—— 1946, Egg-bursters in some more families of polyphagous beetles and some general remarks on egg-bursters. *Proc. R. ent. Soc. Lond.* (A) **21** : 89–97.

Verhoeff, K. W., 1919, Zur Lebens-und Entwicklungsgeschichte sowie Regeneration der *Silpha obscura* und *Phosphuga atrata* (Col.). *Suppl. Ent.* **8** : 41–116.

Weber, H., 1933, *Lehrbuch der Entomologie.* Jena.

—— 1954, *Grundriss der Insektenkunde.* Stuttgart.

Wheeler, W. M., 1889, The embryology of *Blatta germanica* and *Doryphora decemlineata*. *J. Morph.* **3** : 291–386.

Wigglesworth, V. B., 1950, *The Principles of Insect Physiology*, 4th edition. London.

FAUNAL SUCCESSION IN UMBELS OF *CYPERUS PAPYRUS* L. ON THE UPPER WHITE NILE.

By I. W. B. Thornton.

(*University College of Khartoum*).[1]

Introduction.

Weber (1942) called attention to the biocoenose centering about papyrus (*Cyperus papyrus* L.) in the Sadd [commonly known as " Sudd "] region of the White Nile, and listed a number of species of ants collected from papyrus umbels. The present paper is an attempt to examine the fauna of the umbel quantitatively and in more detail, and to describe the succession of animals which occurs as the umbel grows, matures and eventually dies.

Shelford (1913) first developed the concept of faunal succession in natural habitats and described a succession of animal forms correlated with vegetational succession. More recently, a number of synecological studies have been made on small discrete habitats of an organic nature, and the faunal successions occurring during the ageing and decay of these habitats have been described. Examples of studies of this nature are the works of Park (1930) on beach drift, Savely (1939) on dead logs, Mohr (1943) on cattle droppings, Woodroffe (1953) on birds' nests, Park and Auerbach (1954) on tree holes and Winston (1956) on acorns. In the present paper it is proposed to describe the faunal succession which takes place during the life of a single plant.

The umbel of papyrus forms a simple, circumscribed and uniform habitat suitable for studies of a synecological nature. The upright aerial branches, which may be from 3 to 5 m. in length, bear an umbel-shaped inflorescence from half a metre to a metre in diameter. Over a hundred such aerial shoots may arise from one branching system of rhizomes, which rests on the substratum partially or completely immersed in water. Shoots are found at varying stages of development on the same rhizome system ; old branches dry out and die and are continually replaced by new shoots.

Almost permanent flood conditions and a water depth of over 80 cm. are the two factors necessary for the growth of papyrus. These conditions exist on the Victoria Nile in the vicinity of the Lake Kioga swamp (fig. 1), and along the banks of the Albert Nile from Lake Albert to Nimule. Between Rejaf and Bor, papyrus is an occasional component of the riverain vegetation, but north of Bor the flood plain widens, and from here to Lake No, 500 km. further downstream, the river is bordered by permanent swamp dominated by the single species *C. papyrus*. Downstream of Lake No papyrus thins out rapidly, and north of Malakal it occurs only sporadically, its northern limit being at Jebelien.

In the Sadd region along the banks of the Bahr el Jebel, Bahr el Zeraf and Bahr el Ghazal, almost pure stands of papyrus form an impenetrable mass of thick vegetation, and the area of permanent swamp has been estimated at approximately 8000 sq. km. Along the river margins climbers such as *Luffa*

[1] Now at the University of Hong Kong.

cylindrica, Vigna nilotica, Cissus ibuensis and *Ipomea aquatica* compete with the papyrus for light, and occasionally *Melanthera brownei* and *Jussieua diffusa* occur among it. The grass *Vossia cuspidata* is sometimes found as a fringe to the papyrus on the river margin, as is the floating aquatic *Pistia stratiotes*. On higher ground among the papyrus small stands of *Phragmites communis* are

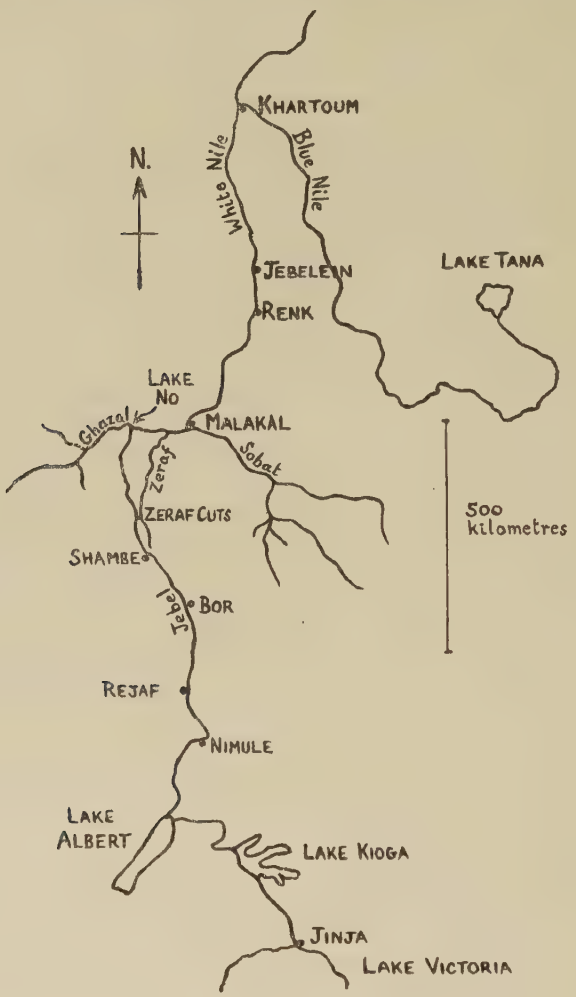


FIG. 1.—Map of the White Nile.

found, and less frequently *Typha australis*. A full description of the flora of this region is given by Tothill (1948) and Migahid (1946).

METHOD.

Two visits were made to the Upper Nile region for the purpose of collecting. During the first, in May and June of 1954, 101 samples were taken at various localities on the Nile from Lake Victoria to Renk. On the second expedition,

during January, 1955, the collecting was limited to 84 samples between Rejaf and Zeraf Cuts.

Samples were taken by cutting off the umbel just below its base, quickly trimming its branches, and plunging all into a vessel containing 70 per cent. alcohol, which was then shaken. Later, the bracts and branches were broken off under a binocular microscope, thoroughly washed, and the larger arthropods removed. The mother liquor was then filtered and the filter residues examined for smaller arthropods such as mites and thrips. Although this method was slow, it had the advantages of being rapid in the field and ensuring the collection of almost the whole of the fauna present in the sample.

The umbels were classified for convenience into five age-groups as follows :

A : Inflorescence enclosed as a bud in sheath-like scales ; rays 7–12 cm. long.

B : Scales opened but umbel not yet opening out; rays 11–18 cm. long.

C : Umbel half-opened ; rays 19–30 cm. long.

D : Umbel fully opened ; rays 29–55 cm. long.

E : Umbel dead, dry ; rays over 50 cm. long.

Where possible, umbels at all stages of maturity were sampled at each station. Each umbel was regarded as one sample.

The fauna of the aerial stalk and rhizomes was not considered. The fauna of the umbel was found to congregate at its base where the bracts and branches form a dense mass from 3 to 5 cm. thick, with crevices between successive bracts and branches.

Checklist of Fauna.

In the following list determinations have been taken as far as is possible with certainty in the present state of knowledge. Where incomplete identifications are given, the specimens were either immature (this applies particularly in the case of spiders), or of species or genera which have yet to be described.

Heavy type indicates occurrence in more than ten samples ; single occurrences are shown thus—(1).

Pseudoscorpionida : Cheliferidae, *Allowithius* sp.

Araneaea : **Salticidae**, *Thyene magdalense* Lessert, *Myrmarachne* sp., *Heliophanus* sp. ; **Thomisidae**, *Xysticus* sp. ; **Gnaphosidae**, *Zelotes* sp. ; Argiopidae, *Araneus* sp. ; Tetragnathidae, *Tetragnatha extensa* L. (1), *Leucage* sp. (1) ; Clubionidae ; Micryphantidae ; Hahniidae (1).

Acarina : Belbidae, *Belba* sp. (1) ; Oppiidae, *Oppia* sp. (1) ; Oribatulidae, *Oribatula* sp. (1), *Zygoribatula* sp. ; **Scheloribatidae**, ***Scheloribates* sp. *A***, *Scheloribates* sp. B ; Galumnidae, *Galumna* sp. (1) ; Tyroglyphidae, *Tyrophagus* sp. ; Rhizoglyphidae ; Eupodidae, *Eupodes* sp. ; Tydeidae, *Tydeus* sp ; **Bdellidae, *Trachimolgus* sp.** ; Cunaxidae, *Cunaxoides* sp. (1) ; Erythraeidae, *Balaustium* sp. ; Macrochelidae, *Macrocheles* sp. (1) ; **Neoparasitidae, *Ololaelaps* sp.** ; Digamasellidae, *Digamasellus* sp. (1), *Asea* sp. ; Arrhenuridae, *Arrhenurus* sp. ; Anisitsiellidae, *Nilotonia* sp. ; **Phytoseiidae, *Typhlodromus* spp.**—***A***, *B* (1), *C*, ***D***, *E* (1), *F*, *G*, *Iphiseius* sp. ; Aceosejidae, " Aceosejinae " (1), " Platyseiinae ", *Kleemannia* sp., *Jordensia* sp., *Lasioseius* sp.

Thysanura.

Collembola : ***Lepidocyrtinus flavo-virens*** Borner, ***Drepaneura* sp.**, *Lepidocyrtus* sp., *Xenylla lesnei* Denis (1).

Orthoptera : Blattidae, *Matabelina abdominalis* (Shelf.).

Corrodentia : **Psocidae, *Archipsocus* sp.**, *Deipnopsocus* sp., *Caecilius* sp.

Thysanoptera : **Thripidae, *Catina papyri*** Faure, ***Trichomothrips bellus*** Priesner, ***Dorcadothrips caespitis*** Priesner, *Sericothrips occipitalis* Hood, *Edissa flava* Faure ; Phlaeothripidae, ***Haplothrips avenae*** Priesner, ***Haplothrips tolerabilis*** Priesner, ***Chiraplothrips* sp.** ; Urothripidae (1).

Trichoptera : Hydropsychidae, *Cheumatopsyche* sp.

Homoptera : **Coccidae, *Steatococcus* sp., *Planococcus* sp.**, *Trionymus* sp., *Rhizoecus* sp., *Aulacaspis* sp., *Lindingaspis* sp., *Coccus hesperidum* L. (1) ; Jassidae ; **Aphidae, *Schizaphis cyperi*** (Van der Goot).

Heteroptera : Pentatomidae, *Delegorguella* sp. (1), *Carbula pedalis* Bergr. (1) ; Lygaeidae, *Cymodema* sp., *Ischnodemus* sp. (1) ; **Tingidae, *Serenthia lineata*** Herv., *Serenthia* spp. A (1), B (1) ; Pleidae, *Plea pullula* Stål.

Lepidoptera : larvae only.

Coleoptera : Carabidae, *Tachis* sp. (1) ; Dytiscidae, *Synchortus* sp. (1) ; Staphylinidae, *Asterus* sp., *Paederus* sp. (1) ; Endomichidae, *Danae* sp. (1) ; Nitidulidae, *Carpophilus* sp. (1) ; Elmidae (1) ; Trichopterygidae (1) ; Corylophidae, *Aposericoderus* sp. A (1) ; Cucujidae,*Laemophloeus* sp. (1), *Silvanolomus denticollis* Rietl. ; Phalacridae, *Olibrus* sp. ; Coccinellidae, *Scymnus* sp. (1) ; Hydrophilidae, *Coelostoma* sp. (1) ; Dascillidae, *Scirtes* sp. (1) ; Buprestidae, *Aphanisticus* sp. (1) ; Lagriidae, *Chrysolagria* sp. (1) ; Anthicidae, *Anthicus* sp., *Tomoderus* sp. A, sp. B ; **Curculionidae,** *Endaliscus* sp. (1), *Aorus anthracinus* Branc., ***Echinocnemus* sp.**, ? genus nr. *Echinocnemus*.

Hymenoptera : Bethylidae, *Goniozus* sp. ; Diapriidae, *Trichopria* sp. (1) ; Pompilidae (1) ; Scelionidae, *Ceratobaeus* sp. ; Encyrtidae, *Thysanus* sp. (1), *Xanthoencyrtus* (*Pholidoceras*) sp. (1) ; Eulophidae (1) ; Mymaridae, *Anaphoidea* sp. (1) ; **Formicidae, *Pheidole megacephala*** F., ***Crematogaster* (*Acrocoelia*) sp., *Acantholepis capensis*** Mayr, *Ponera* sp., *Cardiocondyla wroughtoni bimaculata* Wheeler, *Crematogaster* sp., *Monomorium floricola* Jerd. (1), *Macromischoides aculeata* Maur. (1), *Camponotus* (*Myrmotrema*) sp., *Plagiolepis brunni* Mayr (1).

Diptera : Phoridae, *Diploneura* (*Dohrniphora*) *cornuta* Big. (1) ; Milichiidae, *Desmometopa singaporensis* Kert. (1) ; Borboridae, *Leptocera* sp. (1).

Mollusca : Gasteropoda : Ariophantidae (1).

Succession of the Main Taxa.

In all, 185 papyrus umbels were sampled, at least 20 of each age group, and from these 8125 arthropods were collected. For each taxon, the percentage frequency and average number per sample in each of the five umbel age groups are given in Table I. The percentage frequency is the proportion of samples in any one age group in which a particular taxon is represented, expressed as a percentage. Thus the figures in this part of the Table are comparable horizontally as well as vertically. The maxima for each order of arthropods are in italics, and the close agreement of the two series of maxima indicates that in general the degree of dispersal among the sample units is high, for at whichever

stage of the umbel a particular group of animals is most abundant, it is also most widespread. The homopteran family Coccidae has been treated separately from the rest of the Homoptera in this analysis.

Twenty-six umbels of age groups A, B, C and D were marked in March, 1956, in Uganda, and the rays were measured and the form of the umbel noted at five-day intervals for a period of 37 days. In this way the following estimates were obtained for the duration of each age group : A, 3–7 days ; B, 7–14 days ; C, 10–25 days ; D, over 37 days. It was not possible to obtain an estimate for the duration of stage E. In figure 2 the data of Table I (*a*) are represented

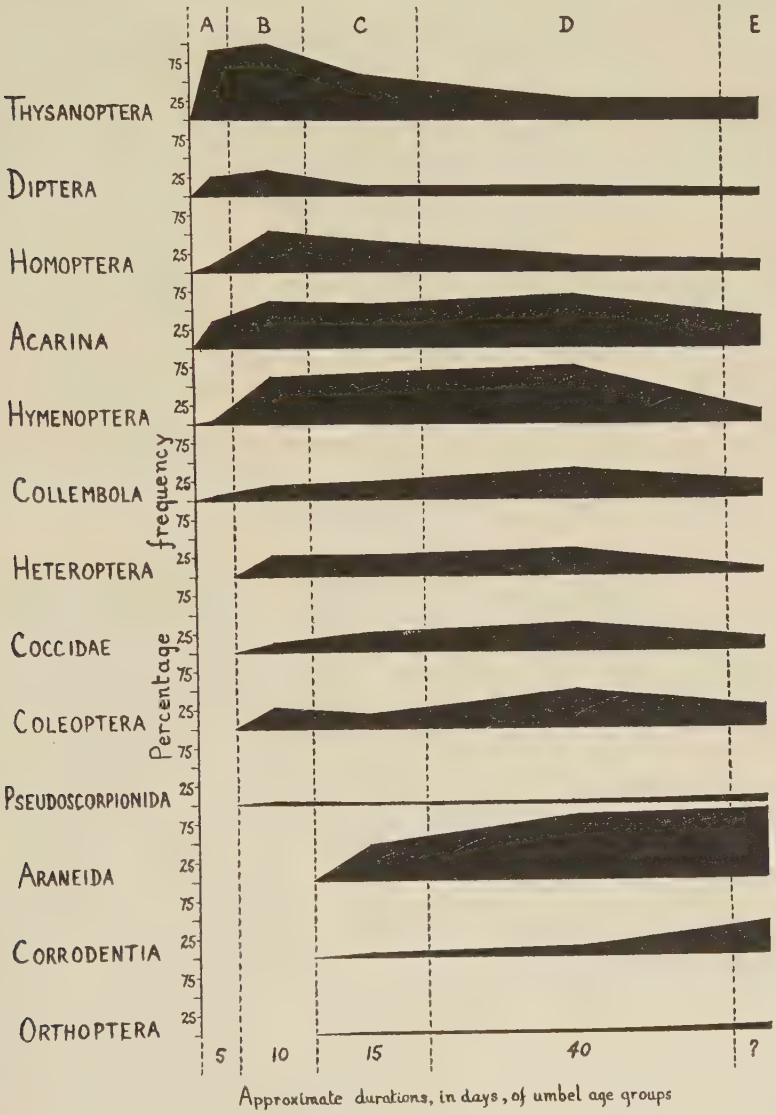


FIG. 2.—Frequency distribution of the main taxa of arthropods in papyrus umbels of various age groups.

graphically, and the relative durations of the various umbel age groups are incorporated.

TABLE I (*a*) and (*b*).—*The occurrence of the main taxa of arthropods in umbels of* Cyperus papyrus.

	(*a*) Percentage frequency.					(*b*) Average number/sample.				
Umbel age groups .	A.	B.	C.	D.	E.	A.	B.	C.	D.	E.
Number of samples .	20	26	60	54	25	20	26	60	54	25
Thysanoptera . .	90·0	*100·0*	60·0	29·6	28·0	24·0	*57·7*	24·2	21·5	0·8
Homoptera . .	10·0	*53·9*	41·7	20·4	12·0	0·7	*15·9*	2·9	0·4	0·2
Diptera . . .	25·0	*34·6*	13·3	13·0	8·0	0·5	*0·7*	0·3	0·4	0·2
Acarina . . .	35·0	61·5	58·3	*70·4*	40·0	0·7	1·8	3·3	*10·0*	3·4
Hymenoptera . .	5·0	61·5	66·6	*75·9*	16·0	*	2·1	2·3	*13·4*	0·6
Collembola . .	5·0	19·2	23·3	*40·8*	24·0	0·1	0·5	0·5	*1·3*	0·4
Heteroptera . .	.	26·9	26·6	*35·2*	8·0	.	0·7	0·6	*0·9*	0·1
Coccidae . . .	.	11·5	25·0	*37·0*	16·0	.	0·3	0·7	*1·9*	0·2
Coleoptera . . .	.	26·9	18·3	*50·0*	28·0	.	0·4	0·3	*1·0*	*1·2*
Araneida . . .	.	.	46·6	*85·2*	*92·0*	.	.	1·2	*4·5*	*3·0*
Pseudoscorpionida .	.	3·8	1·6	3·5	*8·0*	.	*	*	*	*0·4*
Corrodentia . .	.	.	5·0	11·1	*44·0*	.	.	0·1	0·2	*2·9*
Orthoptera . . .	.	.	1·6	2·0	*8·0*	.	.	*	*	*
Thysanura . .	.	.	3·3	.	.	.	.	*	.	.
Lepidoptera . .	.	7·7	3·3	5·5	12·0	.	0·2	*	0·1	0·1
Ephemeroptera .	.	3·8	.	.	.	.	*	.	.	.
Trichoptera . .	.	3·8	.	.	4·0	.	*	.	.	*

Note.—The asterisk indicates presence, but an average number per sample of less than 0·1. The homopteran family Coccidae has been treated as a separate taxon.

The sap-sucking Thysanoptera and Homoptera (mostly aphids) reach their maxima, both in frequency and numbers, at an early stage of the umbel. This stage (B) has been shown to be that at which the growth rate of the shoot is at a maximum (Migahid, 1946) and it is probable that the condition and availability of the sap are optimum. The Hymenoptera (mainly ants) reach both their maxima in the mature umbels and there seems to be little correlation between ants and aphids. Mites are the most frequently occurring group in this habitat, and reach maximum numbers in the mature umbels. The predaceous pseudoscorpions and spiders, and the detritus and fungus feeding Corrodentia, are later arrivals and reach their maxima on the death of the umbel.

For each of the umbel age groups, the average number of individuals of each taxon per sample in which that taxon is recorded, is presented in Table I (*c*). This figure is an index of the population density of the group of animals in the umbels in which it occurs. The Thysanoptera show two maxima for this index, one in age group B where there is 100 per cent. frequency occurrence, and a second in age group D where the frequency is only 29·6 per cent. These figures suggest that two main populations are involved; the first reaching maximum numbers in the early umbel stages and having very good powers of dispersal, the second reaching maximum numbers later, with poorer dispersal but with high population densities where it occurs. By comparing the density

index and percentage frequency, some estimate of dispersal can thus be obtained for each group of animals. The Acarina and Hymenoptera (mainly ants) are fairly well dispersed in umbels of age groups B and C (low density, high frequency) with the main build-up in population density in stage D. The spiders show very good dispersal in the mature and dead umbels, where populations are relatively small. By contrast the Homoptera (mostly aphids) are less frequent even at their maximum, and have relatively high population densities where they occur, indicating relatively poor dispersal. The same applies, to a lesser extent, to the pseudoscorpions and Corrodentia.

TABLE I (*c*).—*Population density indices of the main taxa of arthropods on papyrus umbels at various stages of growth.*

	Umbel age groups.				
	A.	B.	C.	D.	E.
Thysanoptera . .	26·2	57·7	40·3	72·6	3·0
Homoptera . .	7·0	29·5	7·0	1·9	1·3
Diptera . . .	1·8	1·9	2·4	2·7	2·0
Acarina . . .	2·0	2·8	5·6	14·2	8·6
Hymenoptera . .	1·0	3·4	3·5	17·6	4·0
Collembola . .	2·0	2·8	2·1	3·1	1·5
Heteroptera . .	.	2·4	2·4	2·4	1·5
Coccidae . . .	.	2·0	2·7	5·0	1·0
Coleoptera . .	.	1·4	1·7	2·1	4·3
Araneida . . .	.	.	2·5	5·3	3·3
Pseudoscorpionida .	.	1·0	1·0	1·0	5·5
Corrodentia . .	.	.	1·0	2·1	6·6
Orthoptera . .	.	.	1·0	1·0	1·0

REMARKS.

Thysanoptera.

Using this material Faure (1956) described and named *Catina papyri*, a hitherto unknown genus of the suborder Terebrantia near *Exothrips* Priesner ; redescribed *Haplothrips avenae*, originally based on one male and one female taken on oats in Nyasaland ; and provided taxonomic information on six other species.

The suggestion made in the preceding section, that two main populations are involved, is supported on specific determination of the thrips. There is an interesting succession of the three most common representatives, *Catina papyri* Faure, 1956, *Haplothrips avenae* Priesner, 1950, and *Haplothrips tolerabilis* Priesner, 1936. The distribution of these three species on the successive stages of the umbels in the winter collection is shown in Table II, and in figure 3 the larvae of *C. papyri* are graphed separately. *C. papyri* is very common and is probably a plant feeder. Adults are found in the young buds (A and B), larvae appear in stages B and C, there is a sharp decline at stage D, and only very occasional specimens in the dead umbels. *H. avenae* is almost as common as *C. papyri* but does not reach its maximum until age groups C and D, with a sharp decline at E. It is remarkable that no larvae were found which could possibly be of this species. Some species of *Haplothrips* are known to be predaceous and it is possible that adults of *H. avenae* invade the umbel once a large population

of animals is established there, feed for a time on small prey, and leave the umbel as the larger predators begin to increase in numbers, ovipositing in some other habitat. It is evident that as the population of *H. avenae* increases, that of *C. papyri* declines, and the two populations may possibly be inter-related as predator and prey. *H. tolerabilis*, which is frequent in the winter collection only, was first described from *Cymbopogon* grass in the Sudan. A species of *Cymbopogon* is a component of the intermediate grasslands fringing the permanent swamp of the Sadd region of the Sudan.

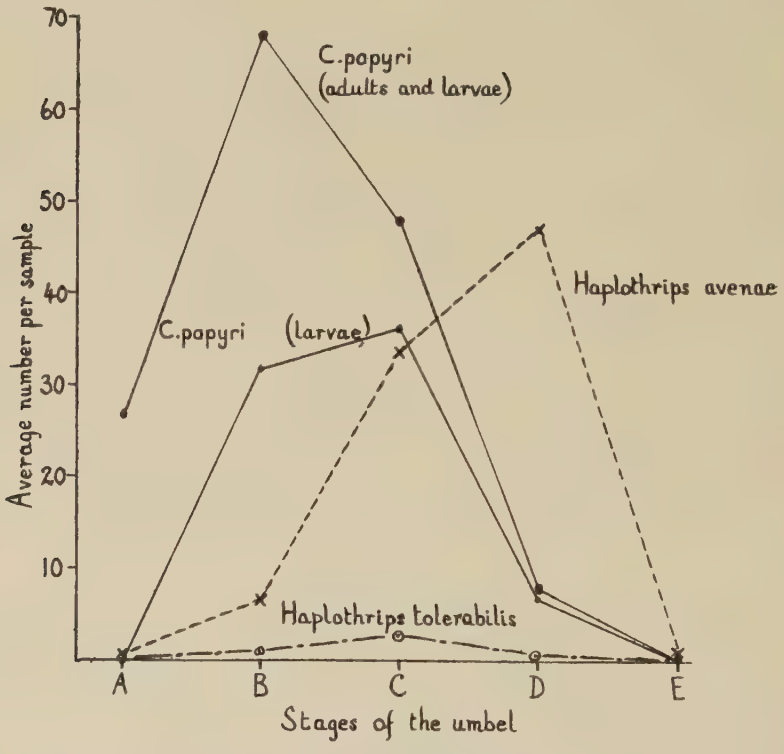


Fig. 3.—Distribution of three species of thrips in papyrus umbels at various stages of maturity.

Over 4500 specimens of thrips were collected, but only two pupae and one prepupa were found. It is most unlikely that pupae were missed in the sampling. The females probably lay eggs for a week or more, with a succession of hatchings, so that some overlap of the different stages would be evident if pupation took place in the umbel. Some thrips species are known to pupate on the food plant, others on the ground. It seems likely that in this case pupation takes place among the rhizome mass at the base of the plant.

Of the less ecologically important species dealt with by Faure (1956), *Trichromothrips bellus* and *Dorcadothrips caespitis* are probably grass feeders. *T. bellus* is found occasionally on papyrus in the Sadd, and *D. caespitis* at Lake Victoria, Rejaf and the Sadd, both species occurring on young growing heads. *Sericothrips occipitalis* is the common bean thrips of South Africa and Rhodesia,

TABLE II.—*The distribution of three species of thrips in umbels of papyrus at various stages of maturity, winter* 1954–55.

	Umbel age groups.				
	A.	B.	C.	D.	E.
Number of samples . .	15	15	16	20	18
Average number/sample—					
Catina papyri . . .	26·9	67·9	47·7	8·1	0·1
Haplothrips avenae . .	0·7	6·5	33·7	47·1	1·0
Haplothrips tolerabilis . .	.	0·9	2·7	0·5	.
Percentage frequency—					
Catina papyri . . .	93·3	100·0	93·8	55·0	11·0
Haplothrips avenae . .	33·3	80·0	81·3	60·0	33·0
Haplothrips tolerabilis . .	.	40·0	56·3	30·0	.

and was only taken at the Rejaf station. *Edissa flava*, described from kikuyu grass in Pretoria, also occurred only at Rejaf.

Homoptera.

The Homoptera of Table I consisted mostly of the aphid *Schizaphis cyperi*, which occurred commonly in both summer and winter samples at Rejaf and in the Sadd, mainly on umbels of age groups B and C. Jassids were only occasionally present on the early stages at Rejaf and at Bor. The coccids, treated separately in Table I, were not found in the closed buds and, in contrast to the aphid, reach a maximum in the mature umbels. This may be due in part to their relatively poor powers of dispersal, so that in the absence of appreciable immigration the population would build more slowly and have a later climax. There are no previous records from papyrus in Africa, and many undescribed species were collected. *Coccus hesperidum* is a polyphagous species with a world-wide distribution.

Diptera.

Most of the Diptera collected were in the larval stage. Many adults, visitors of the papyrus, were probably excluded by the sampling technique. Although the papyrus swamp obviously provides plenty of decomposing organic matter for the Phoridae and Borboridae, only single specimens were taken.

Acarina.

The most frequent and most numerous family, the Phytoseiidae, is represented by a number of undescribed species of the genus *Typhlodromus*, and reaches very marked maxima in both numbers and frequency in the mature umbels. This family, like the Gamasidae, Tydeidae, Bdellidae and Cunaxidae, probably feeds mainly on thrips and aphids as well as psocids, collembolans and saprophagous mites. The saprophagous oribatids and tyroglyphids are most numerous in umbels of age groups C and D.

Hymenoptera.

The relatively high population densities found in the mature umbels are due to the presence of ants, of which this group largely consists. *Pheidole mega-*

cephala, the commonest species, occurs from Lake Victoria to Lake No. *Acantholepis capensis* was found from Rejaf to Lake No, *Crematogaster* (*Acrocoelia*) sp. at Bor and Renk, and *Camponotus* (*Myrmotrema*) sp. at Lake Victoria and Shambe. These four species can be regarded as permanent residents of the papyrus umbel, this being the only available nesting site in the Sadd region.

Cardiocondyla wroughtoni bimaculata was found at Lake No, *Plagiolepis brunni* at Jonglei, *Macromischoides aculeata* at Lake Victoria and *Monomorium floricola* at Bor. Weber (1942) records the following species in addition to the four mentioned in the previous paragraph: *Camponotus* (*Myrmoturba*) *maculatus*, *Leptothorax angulatus* and *Cataulacus pygmaeus*.

The Scelionidae, egg parasites of the spiders in the later umbel age groups, and the Pompilidae, which prey on spiders, are important components of the fauna, although not numerous. The Diapriidae are known to parasitise dipterous larvae, and *Goniozus* species usually attack lepidopterous larvae. The Encyrtidae and Eulophidae were found in late stages of the umbels and possibly prey on coccids and aphids. The mymarids occurred with tingid bugs in an umbel at stage B.

Collembola.

Lepidocyrtinus flavo-virens was present in umbels of all age groups both at Rejaf and in the Sadd region, and was the commonest collembolan encountered in this habitat. It is of widespread occurence in Africa and is not peculiar to papyrus umbels. A species of *Drepaneura*, shortly to be described by Goto, occurred on Lake Victoria and quite commonly in the Sadd, but was only recorded from mature umbels. A species of *Lepidocyrtus*, also to be described by Goto, was present in only two samples in the Sadd, and *Xenylla lesnei* in only one at Bor.

Heteroptera.

The Tingidae were represented by three species of *Serenthia*, two of which occurred each in only one sample; the third, *Serenthia lineata*, occurred in 35. In Table III the relative numbers and frequency of this species and the aphid *Schizaphis cyperi* are compared. *S. lineata*, unlike the aphid, is absent from the closed bud (A), and does not show such well marked maxima in the growing umbels (B and C). Apparently the tingids are unable to compete with the aphids in the young growing heads, but can maintain about equal numbers in the mature umbels (D). Perhaps their larger size makes them less liable to predation.

TABLE III.—*Relative numbers and frequency of* Schizaphis cyperi *and* Serenthia lineata *on papyrus umbels of various age groups.*

	Umbel age groups.				
	A.	B.	C.	D.	E.
Number of samples . .	20	26	60	54	25
Average number/sample—					
Schizaphis cyperi . .	0·7	15·4	2·5	0·7	0·1
Serenthia lineata . .	0·0	0·4	0·3	0·6	0·1
Percentage frequency—					
Schizaphis cyperi . .	10·0	50·0	38·3	14·8	8·0
Serenthia lineata . .	0·0	19·0	18·3	26·0	8·0

Coleoptera.

The beetles were present both as larvae and adults, reaching a maximum in the mature and dead umbels. Only the Staphylinidae, Cucujidae, Phalacridae, Anthicidae and Curculionidae were represented in more than two samples. The commonest beetle was a weevil, a species of *Echinocnemus*, and occurred mainly in mature umbels between Bor and Renk. It is probable that the papyrus umbel is its natural habitat. Although the species of *Danae* occurred in only one sample, both larvae and pupae were present as well as adults. The umbel of papyrus may also be the normal habitat of the two species of *Tomoderus*. *Silvanolomus denticollis* is a stored products insect of which the natural habitat is not yet known.

Araneida.

The Salticidae were by far the most frequent and most abundant family, followed by the Thomisidae. The former family reaches its greatest numbers in umbels at stages D and E, the latter in stage D with a decrease in E. The Gnaphosidae were only taken on the summer expedition and show no clear maximum. The Clubionidae were almost as frequent as the Thomisidae in the growing umbels (C), but only occurred once in the mature heads, and not at all in the dead umbels.

Spiders were caught with ants, coccids, adult Diptera and mites as prey. Most of the specimens were immature, hence the difficulty in specific determination.

Pseudoscorpionida.

There is little doubt that the pseudoscorpions are carried on to fresh umbels by insects (phoresy). They have been observed to prey on thrips and mites (Rafalski, *private communication*).

Corrodentia.

The commonest psocid was a species of *Archipsocus*, which was present mainly in dead umbels in the winter collection from the Sadd region. It was absent at Rejaf, but present in one sample from Lake Victoria. As many as 47 specimens were taken in one sample. Psocids are fungus and detritus vegetable feeders, and it is not surprising that maximum numbers and frequency are found in the dead umbels.

Discussion.

The fauna of the papyrus swamp of the Sadd region may be expected to change in future years. The projected Jonglei Canal (*Anon*, 1954) will divert the White Nile round the Sadd where present losses through transpiration and evaporation amount to 50 per cent. As gradually drier conditions are provided, and cultivation introduced, papyrus will become much less important as a habitat, and may even die out. This enforced change of habitat is likely to be accompanied by major readjustments of the present fauna to the new environmental conditions.

The succession of phytophagous, predaceous and saprophagous groups has already been noted. The causes of succession of various species of plant feeders, e.g. *Schizaphis cyperi* and *Serenthia lineata*, are obscure. There is little doubt

that as the umbel ages the condition and availability of its sap will change, and this may have a differential effect on the sap-sucking fauna. Degree of tolerance to predators may also differ from species to species.

The umbel of papyrus cannot be regarded as anything like a closed community. Usually, the vegetation is so thick that mature umbels touch, so that emigration from one to the other is an easy matter even for apterous species. The growing umbels (stages A, B and C) are borne on shorter branches, so that they are rather more isolated, although by no means completely so. It is very probable that when conditions in a particular umbel have become unsuitable, a species may be driven out and on to another one at a different stage of maturity. If this is so, the fauna of a region of papyrus swamp will consist of species populations which periodically move from one umbel to another at an optimal stage of growth. Although complete food relationships are difficult to establish from the available data, the richness and succession of the fauna indicate that the papyrus umbel is the site of an intricate food web, the pattern of which changes as the umbel grows, matures and dies.

Summary.

The papyrus swamp is described and its extent on the Upper White Nile indicated.

From data obtained by sampling papyrus umbels at different stages of growth, it is demonstrated that a succession of arthropods occurs in the umbel as it grows, matures and dies. The succession is described, and a faunal list is given.

Comments are made on various aspects of the succession, and the dynamic nature of the species populations is discussed.

Acknowledgments.

It is a pleasure to acknowledge the facilities provided by the Hydrobiological Research Unit of the University College of Khartoum. This work was undertaken as part of a general programme of investigations on riverain biology carried out by that unit.

My thanks are also due to the following for taxonomic identifications: The Commonwealth Institute of Entomology; Mr. J. Balfour-Browne (Coleoptera); Dr. J. C. Faure (Thysanoptera); Mr. H. E. Goto (Collembola); Mr. J. Rafalski (Pseudoscorpionida) and Mr. C. F. Roewer (Araneida).

References.

Anon., 1954, *The Equatorial Nile Project and its effects in the Anglo-Egyptian Sudan.* Sudan Government Publication.

Faure, J. C., 1956, Thysanoptera from papyrus in the Sudan. *J. ent. Soc. S. Afr.* **19** : 100–17.

Migahid, A. M., 1946, *Report on a botanical excursion to the Sudd region.* Cairo. Fouad I University Press.

Mohr, C. O., 1943, Cattle droppings as ecological units. *Ecol. Monogr.* **13** : 275–98.

Park, O., 1930, Studies in the ecology of forest Coleoptera. Seral and seasonal succession of Coleoptera in the Chicago area, with observations on certain phases of hibernation and aggregation. *Ann. ent. Soc. Amer.* **23** : 57–80.

Park, O., and Auerbach, S., 1954, Further study of the tree-hole complex with emphasis on quantitative aspects of the fauna. *Ecology* **35** : 208–22.

Savely, H. E., 1939, Ecological relations of certain animals in dead pine and oak logs. *Ecol. Monogr.* **9** : 321–85.

Shelford, V. E., 1913, Animal communities in temperate America. *Bull. geogr. Soc. Chicago* **5** : 1–368. (Reprinted 1937, University of Chicago Press).

Tothill, J. D., 1948, *Agriculture in the Sudan.* Oxford University Press.

Weber, N. A., 1942, A biocoenose of papyrus heads (*Cyperus papyrus*). *Ecology* **23** : 115–9.

Winston, R. W., 1956, The acorn microsere, with special reference to arthropods. *Ibid.* **37** : 120–32.

Woodroffe, G. E., 1953, An ecological study of the insects and mites in the nests of certain birds in Britain. *Bull. ent. Res.* **44** : 739–72.

THE BRITISH SPECIES OF *TRICHOCERA* (DIPTERA: TRICHOCERIDAE).

By B. R. Laurence.

(*London School of Hygiene and Tropical Medicine*).

Although only nine species of *Trichocera* are recorded from Great Britain, and although the species are sufficiently common to have been given the popular name of " winter gnats ", some of the species are difficult to separate. Because of the difficulty in identification it is probable that the biology of some of the species has been confused. *Trichocera saltator* Harris breeds commonly in cow dung both in the south and north of England. Another species, *T. regelationis* L., has been recorded as breeding in cow dung in Scotland (Cuthbertson, 1926, 1929). The larvae of both species may have the same habitat but it is possible that one species has been misidentified.

Keys to the British species have been given by Edwards (1938) and these have been followed by Freeman (1950). These keys are unsatisfactory for the separation of certain species, in the reliance placed on venational characters where relative lengths of certain wing veins and cells are compared. It is well known that specimens of *Trichocera* are often found showing abnormalities of the venation, such as the presence of additional veins, and also the relative lengths of the veins and cells in normal individuals are more variable than is indicated in the keys. *Trichocera fuscata* Meigen has been separated from *T. saltator* Harris for the sole reason that Edwards found Meigen's types to possess R_{2+3} shorter than the first section of R_2. A series of *T. saltator* bred from cow dung showed that the proportions of these veins were variable. Alexander (1952) has commented on the unsatisfactory use of the proportions of the veins as a major key character. The same type of criticism also applies to the use of the shape of cell M_1 as a key character. The shape of this cell is variable in *Trichocera hiemalis* Degeer and in *T. saltator*, yet it is used in separating the species. In addition, the presence of clouding over the cross-vein *r–m* used to distinguish *T. regelationis* appears to be unsatisfactory. The clouding varies in intensity in this species, and slight clouding of this cross-vein is present in individuals of other species.

Oldroyd and Ribbands (1936) showed that the use of differences in the distribution of setae on the wings of Chalcids was taxonomically unsatisfactory, but Alexander (1927) described differences between new species of *Trichocera* in the arrangement of setae in the subcostal, median and cubital veins, though later he appears to have abandoned this method of separating species. Nevertheless detailed study of the distribution of setae on the subcosta and radial sector shows that the arrangement of setae on these veins (that on other veins has not been examined in detail) is of value in separating the species of *Trichocera*.

It has been found that males of the British species can be separated into three groups, characterised by the presence or absence of numerous ventral setae on the subcosta and radial sector.

PROC. R. ENT. SOC. LOND. (A) 32. PTS. 7–9. (OCT., 1957).

Group 1 : Subcosta with numerous ventral setae (30–100); radial sector usually not bare beneath. *T. annulata* Mg., *T. maculipennis* Mg., *T. regelationis* L., *T. major* Edw.

Group 2 : Subcosta with numerous ventral setae (25–60); radial sector usually bare beneath. *T. hiemalis* Deg., *T. parva* Mg., *T. rufescens* Edw.

Group 3 : Subcosta without or with few ventral setae (0–25); radial sector usually bare beneath. *T. saltator* Harris (*T. fuscata* Mg.).

Along the subcosta the dorsal setae are slightly longer than the ventral and do not reach much beyond the middle cross-vein Sc_2. In Groups 1 and 2 the ventral setae may extend to the base of the wing, and approximately half the ventral setae lie on each side of Sc_2. In Groups 1 and 2, also, the setae are usually closer together than the length of each seta, and when numerous the setae may be so closely crowded that some may lie side by side. In Group 3 the subcosta is either bare beneath, or the ventral setae are concentrated mainly at Sc_2 and again towards the end of the subcosta at the costa. Each species has a characteristic distribution pattern of dorsal and ventral setae on the subcosta (figs. 1 and 2); the species of Group 1 possessing most, and those of Group 3 least, setae. When the mean numbers of dorsal and ventral setae were calculated for each species (excluding *T. maculipennis* Mg. which was not available for detailed examination) it was found that these mean numbers were closely correlated (correlation coefficient $r = + 0{\cdot}92$), indicating no sudden change to bareness of the veins in the evolution of the species (fig. 1).

Along the radial sector the dorsal setae are continuous in all species up to shortly before the fork into R_{2+3} and R_{4+5}. Here, in place of setae, are found one to three circular pits on the vein. Beyond the pits and towards the fork of the vein are usually a few normal setae. Opposite the dorsal pits, usually opposite the pit furthest from the fork, is a ventral pit, and the vein is often widened at this point. Ventral setae are present along the main part of the vein from the ventral pit towards the base of the wing only normally in the species belonging to Group 1, but a few ventral setae are present in all species between the ventral pit and the fork of the vein (Table I). In the species belonging to Groups 2 and 3 the radial sector is normally bare beneath from the ventral pit towards the base of the wing. When ventral setae are present along the radial sector the cross-vein *r–m* also usually bears setae. In Groups 2 and 3 both the radial sector beneath and *r–m* are usually bare. Males of *T. rufescens* Edw. are exceptional in that the radial sector is usually bare beneath and *r–m* usually carries setae.

The survey of the setation of the veins was based upon an examination of male specimens; as the only reliable taxonomic character at present in some species is the structure of the male genitalia, females of *Trichocera* are more difficult to determine than are the males. However, an examination of the wings of females of *T. annulata* Mg., an easily recognised species, and of *T. saltator* Harris, females of which had been bred associated with males, showed that the pattern of distribution of setae on the veins in females is similar to that of males of the same species, but that females tend to possess more setae (Table I, fig. 2), and so tend to lie outside the range shown for males in Table I. Nevertheless, the identification of females may be assisted by removing and mounting a wing, and counting the number of dorsal and ventral setae on the subcosta and radial sector.

The use of the setal distribution pattern on the veins has raised certain problems concerning the previous nomenclature of Edwards (1938) and Freeman (1950). Edwards described as var. *rufulenta* what he considered to be a female

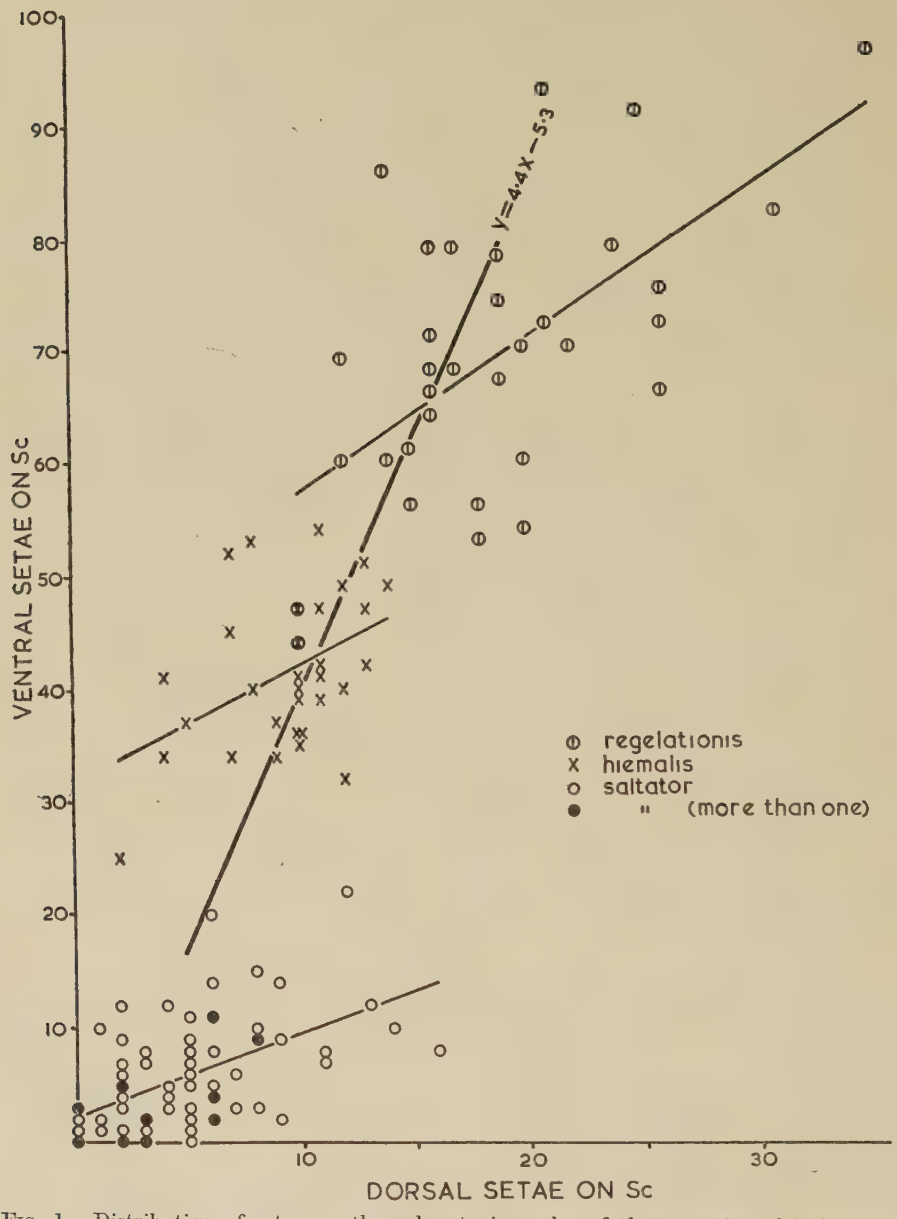


Fig. 1.—Distribution of setae on the subcosta in males of three species of *Trichocera*. The line $y = 4{\cdot}4\ x - 5{\cdot}3$ is fitted to the means of *all* British species (except *T. maculipennis*) and represents the evolutionary trend of the species. Other lines fitted to the points shown.

variety of *T. saltator* Harris. These females are characterised by a very short ovipositor and reddish-brown coloration. No individuals of this variety were found among about 200 females of *T. saltator* bred from cow dung. Although other species of *Trichocera* may show reddish coloration in some specimens (*T. hiemalis*, *T. parva*), or in most individuals (*T. regelationis*, *T. rufescens*, *T. major*), all bred specimens of *T. saltator* were found to be uniformly blackish-brown. The var. *rufulenta* also differs from *T. saltator* in that numerous ventral setae (30–61) are present along the subcosta in *rufulenta* (fig. 2). From the distri-

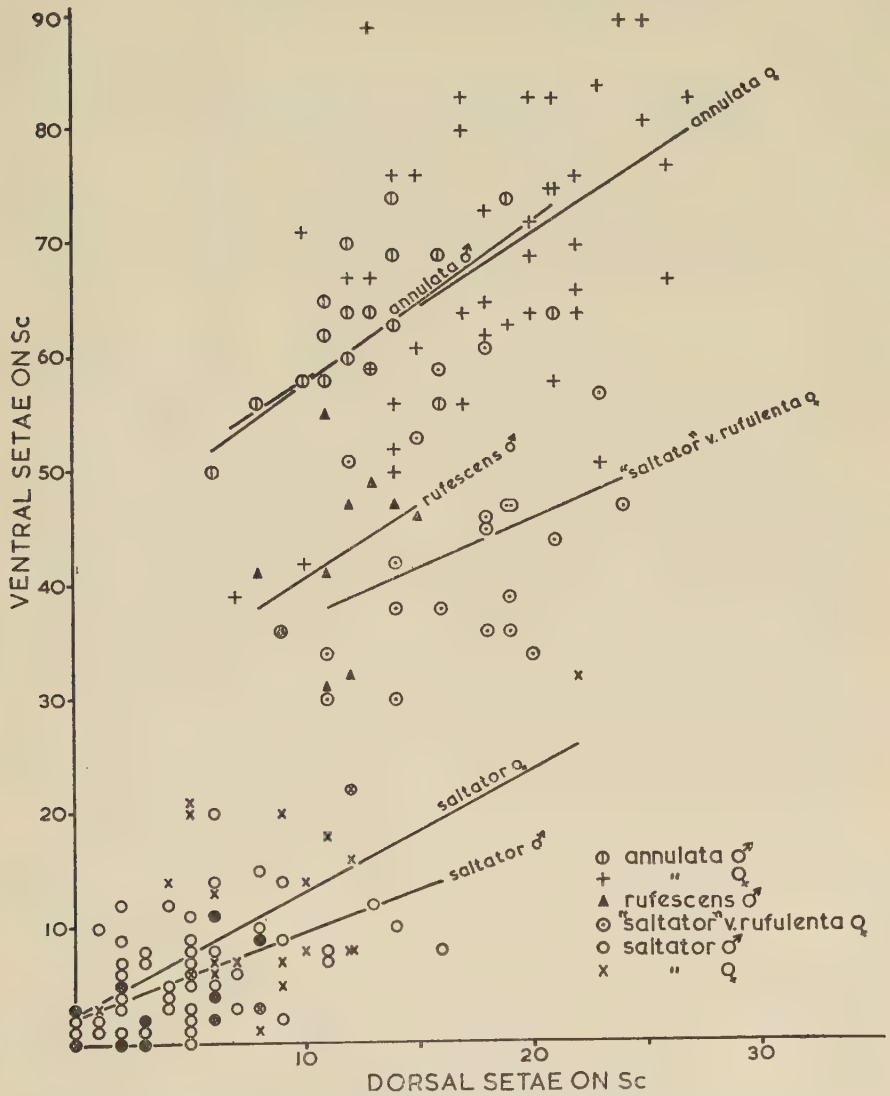


Fig. 2.—Distribution of setae on the subcosta in males and females of *Trichocera annulata* and *T. saltator*, and also males of *T. rufescens* and females of *T.* "*saltator*" var. *rufulenta*. Lines fitted to the points shown.

bution pattern of setae in *rufulenta* the closest relatives of this variety are *T. parva*, *T. hiemalis*, and *T. rufescens*, excluding *T. major* which is too large. The coloration of *T. rufescens* resembles that of *rufulenta*, and the distribution of setae on the subcosta and radial sector are very similar (Table I and fig. 2). *T. rufescens*, as described by Edwards, differs from *rufulenta* in the presence of a yellow, not dark, scape of the antenna. Some male *Trichocera*, referable to *T. rufescens* from the structure of the male genitalia, were found to have the scape of the antenna brown and not at all yellowish. As the colour of the scape does appear to vary in the males of *T. rufescens*, the variety named *rufulenta* by Edwards is more probably to be attached to *T. rufescens*.

TABLE I.—*British species of* Trichocera—*mean number and variation* (*range*) *of dorsal and ventral setae along wing veins* Sc *and* Rs.

Species.	Number of individuals.	Ventral setae on *Sc.*	Dorsal setae on *Sc.*	Ventral setae on *Rs* (except base of R_{2+3}).	Dorsal setae on *Rs.*
			Males.		
GROUP 1—					
regelationis . .	33	69·2 (44–96)	19·0 (10–35)	10·7 (2–17)	23·7 (16–32)
annulata . . .	19	61·7 (36–74)	12·7 (6–21)	5·0 (0–11)	23·0 (16–30)
major . . .	7	50·7 (38–65)	11·6 (6–18)	4·4 (1–9)	18·1 (12–29)
GROUP 2—					
rufescens . . .	10	42·5 (31–55)	11·6 (8–15)	0·1 (0–1)	18·2 (14–22)
parva . . .	11	40·2 (25–58)	9·9 (6–17)	0	13·2 (10–15)
hiemalis . . .	31	41·4 (25–54)	9·5 (2–14)	0·6 (0–5)	13·2 (6–27)
GROUP 3—					
saltator . . .	70	5·7 (0–22)	4·8 (0–16)	0·04 (0–1)	15·9 (7–24)
			Females.		
GROUP 1—					
annulata . . .	41	69·0 (39–90)	18·4 (7–27)	8·1 (0–15)	26·9 (16–38)
GROUP 2—					
" *saltator* " var. *rufulenta*	21	43·5 (30–61)	17·1 (11–24)	3·4 (0–12)	23·8 (16–28)
GROUP 3—					
saltator . . .	25	10·9 (0–32)	8·0 (0–22)	0·8 (0–12)	20·6 (10–32)

Specimens of *T. maculipennis* were not available for detailed examination.

Examination of males and females of *Trichocera* bred from cow dung in company with *T. saltator* but possessing R_{2+3} shorter than the first section of R_2, and hence referable to *T. fuscata* in previous keys, showed that the subcosta and radial sector were bare, as in typical *T. saltator*. The male genitalia were also identical with the genitalia of *T. saltator*. *Trichocera fuscata* Meigen, 1818, should therefore be treated as a synonym of *T. saltator* Harris, 1776, as suggested by Laurence, 1956.

An additional character of some value in separating the species, which has not been recorded by previous authors, is the shape of the pregenital sternite in the males. Males of *T. hiemalis* have the posterior border of this sternite convex and rather protuberant, whereas in the other species examined the posterior border of the sternite is concave.

Edwards (1938) suggested the possible presence in Britain of the northern species *T. lutea* Becker and *T. forcipulata* Nielsen, the males of which have distinctive genitalia. Neither species was present in large numbers of *Trichocera* captured by Dr. C. B. Williams in a light trap in Scotland.

The key given by Freeman (1950) may be amended as follows : (it should be realised that exceptional individuals may be found which do not show all the characters given and that females are less certainly determined than are males).

2 Abdomen more or less distinctly banded 3
Abdomen unicolorous or at most with the tip pale 4

3 Posterior margins of abdominal segments pale ; wings clouded over base of *Rs* and over cross-veins. Wing length 7–8 mm. **T. maculipennis** Meigen
Anterior margins of abdominal segments pale ; wings clear although slight clouding may be present on *r-m* and other cross-veins. Wing length 5–8 mm. . . . . **T. annulata** Meigen

4 Few (less than 25) or no ventral setae along *Sc* ; *Rs* bare beneath (except close to fork) ; male styles without basal tubercle, parameres long; blackish species. Wing length 5·5–8 mm. . . . . **T. saltator** Harris
Numerous (more than 25) ventral setae along *Sc* ; *Rs* with or without ventral setae along its length ; if without, then male styles with basal tubercle, or brownish species with parameres short 5

5 R_{2+3} shorter than first section of R_2 ; large brown species ; females with long slender cerci ; male styles long and slightly sinuous, parameres very short and joined for most of their length. Wing length 6–9·5 mm. . . . . **T. major** Edwards
R_{2+3} longer or equal to first section of R_2 ; female and male genitalia not as above 6

6 Cell M_1 longer, more than twice as long as broad, nearly parallel sided but widening apically ; *r-m* with setae ; male styles without basal tubercle 7
Cell M_1 shorter, usually not more than twice as long as broad and not parallel sided, widening apically ; *r-m* bare ; male styles with basal tubercle 8

7 *Rs* with a row of ventral setae or with scattered ventral setae along the vein ; *Sc* with very numerous ventral setae (40–100 +) ; cloud usually present over *r-m* extending over wing membrane ; parameres long. Wing length 4·5–8 mm. . . . **T. regelationis** Linnaeus
Rs bare beneath (except close to fork), if with a few setae along the vein then *Sc* with fewer ventral setae (30–65) (see figs. 1 and 2) ;

no cloud over *r-m* extending over the wing membrane ; parameres short (var. *rufulenta* Edwards has very short cerci). Wing length 5–7 mm. . . . . **T. rufescens** Edwards

8 Larger species ; male pregenital sternite convex posteriorly and rather protuberant ; basal projections of coxites forming a complete bridge ; parameres short. Wing length 4·5–6·5 mm. . . . **T. hiemalis** Degeer

Smaller species ; male pregenital sternite not convex posteriorly or protuberant ; basal projections of coxites separated in middle ; parameres long. Wing length 4–5·5 mm. . . . . **T. parva** Meigen

Acknowledgments.

In particular I am indebted to Mr. B. R. Baker, Mr. D. Bryce and Dr. C. B. Williams who have sent me material from Berkshire, Yorkshire and Inverness-shire respectively. The staff of the British Museum (Natural History) have given me every facility to examine specimens in the collection.

References.

Alexander, C. P., 1927, New or little known Nearctic species of Trichoceridae. *Canad. Ent.* **59** : 66–73.

—— 1952, Undescribed species of nematocerous Diptera. Part 1. *Bull. Brooklyn ent. Soc.* **47** : 88–94.

Cuthbertson, A., 1926, Studies on the Clyde crane-flies. Larval habitats of some local species. *Ent. mon. Mag.* **62** : 84–88.

—— 1929, Studies on Clyde crane-flies, VIII. The seasonal prevalence of crane-flies (Tipuloidea, Dipt.) in the west of Scotland. *Entomologist* **62** : 270–3.

Edwards, F. W., 1938, British short-palped crane-flies. *Trans. Soc. Brit. Ent.* **5** : 1–168.

Freeman, P., 1950, Trichoceridae *in* Coe, R. L., Freeman, P. and Mattingly, P. F. *Handbooks for the Identification of British Insects*, **9** (2) *Diptera.* London.

Laurence, B. R., 1956, On the life history of *Trichocera saltator* (Harris) (Diptera, Trichoceridae). *Proc. zool. Soc. Lond.* **126** : 235–43.

Oldroyd, H. and Ribbands, C. R., 1936, On the validity of trichiation as a systematic character in *Trichogramma* (Hym. Chalcididae). *Proc. R. ent. Soc. Lond.* (B) **5** : 148–52.

A STUDY OF THE GROWTH AND FEEDING HABITS OF THE LARVAE OF FOUR SPECIES OF CADDIS FLIES.

By Hilmy M. Hanna.

(*Zoology Department, University of Manchester*).

Introduction.

Apart from the work of Nielsen (1942, 1948, 1950), no study has been made of the growth of caddis larvae. On the other hand, the food of these larvae has been the subject of many studies—by McLachlan (1863), Lauterborn and Rimsky-Korsakov (1903), Siltala (1907), Thienemann (1908), Wesenberg-Lund (1910, 1911), Noyes (1914), Lloyd (1915, 1921), Alm (1926), Gätjen (1926), Popowa (1927), Martynov (1930), Neave (1933), Glasgow (1936), Slack (1936), Nielsen (1948), Badcock (1949), Jones (1949, 1950), Khalil (1953) and Philipson (1953). All these authors either dissected the larvae or pressed the contents from the gut of growing or fully-grown larvae over a short period of larval life. None of them considered the possibility of seasonal variations in the diet of the larvae. Slack (1936) collected his larvae between April and June and listed the number of individuals in which each type of food organism occurred. This method is unlikely to give a true picture of the composition of the food if this varies from month to month. Jones (1950) listed the percentages of larvae in which each food item occurred. Again, as with Slack's method, it might not show the relative proportion of food items. Although Badcock and Jones mention the time of collection, they have not considered the possibility of seasonal variation. Murphy (1919) discovered that the larvae of *Brachycentrus nigrosoma* changed their feeding habits as they grew older. In order, therefore, to give a true picture, I made a quantitative study of the feeding habits of the larvae of four species of caddis flies throughout their larval life. A study was also made of the growth of the larvae and this was correlated with the feeding habits. Observations were also made on the life cycles of these species.

Method.

This investigation has been carried out on *Limnephilus politus* McLachlan, *Molanna angustata* Curtis, *Limnephilus marmoratus* Curtis and *Anabolia nervosa* (Curtis). The larvae of *L. politus* and *M. angustata* were collected from an open pool at Heaton Mersey near Manchester; the other two species were obtained from another open pool in the same area.

Details of the growth were obtained by collecting about a hundred larvae every month, by sweeping the bottom of the ponds with a net. Samples of the vegetation were examined and the larvae present collected. The larvae were measured wet to the nearest millimetre from the anterior end of the fronto-clypeus to the posterior margin of the tenth abdominal segment. Pupae and adults were also collected in those months when they were present. In order to study the feeding habits, the larvae were dissected month by month, and the mid-gut carefully removed and opened by fine needles in 5 c.c. of water in a small petri dish. The detritus was unravelled with fine needles until a standard thickness and appearance, confirmed by microscope examination, was obtained.

The suspension was transferred to a tube and then shaken thoroughly so that food items might be evenly distributed ; 0·2 of a c.c. was then transferred by a micro-pipette to a slide on which a wooden ring was fixed, so that the food items would be distributed over the same area at every time of examination. The slide was viewed under a standard monocular low-power microscope, fitted with a squared eye-piece. The field of vision was equal to 64 squares, and the number of diatoms, volvocales, chlorococcales and desmids in this field was recorded. The proportion of the field of vision covered by detritus or dead leaves was also recorded. The filamentous algae presented a particularly difficult problem because they vary in length : for this reason a standard length was taken as a unit and the number of units present was determined. The slide was then moved at random to a second area and the process repeated until ten areas had been examined and the means were then calculated. From a consideration of the area of the slide in which the food items were contained it was possible to calculate the total amount of each food item in the mid-gut.

The larvae were classified into groups of similar length to determine (*a*) differences in the composition of the food of larvae of different sizes at various times of the year and (*b*) the seasonal variations in the composition of the food of larvae of the same size. The tables which contain these results are included in an unpublished thesis (Hanna, 1954).

Limnephilus politus McLachlan.

The percentage of larvae of *Limnephilus politus* in each 2 mm. length class is shown in figure 1.

The larvae were found in all months of the year except June and July. In December the pond was covered with ice and a small number of larvae was obtained but the records of these are not shown in figure 1. There was very little growth in winter and, at the same time, there was a drop in the amount of detritus and in the number of diatoms eaten. The larvae grew mainly from March to April and from August to September and in the meantime there was a considerable rise in the amount of detritus and in the number of diatoms in the mid-gut. There was a decline in the relative increase in size of larvae from April to May, and in that period there was a drop in the amount of detritus and diatoms found in the mid-gut.

The pupae of *L. politus* were found with the larvae in the third week of May and were obtained until the first week of July. In the laboratory, at room temperature, the pupal period lasted about three weeks. The adults were collected from early June until late July and were observed resting on the vegetation near the pond and only flew if disturbed. There was only one generation a year.

Molanna angustata Curtis.

The percentage of *Molanna angustata* larvae in each 2 mm. length class is shown in figure 2.

The larvae were found in all months of the year except June. No specimens were collected in December, January and February and it appears that the larvae migrate into deep water during this period. Between November and March little change in the population took place, indicating that there was little growth in winter. The larvae grew mainly between July and November when there was an abundant food supply of detritus, dead leaves, diatoms, volvocales

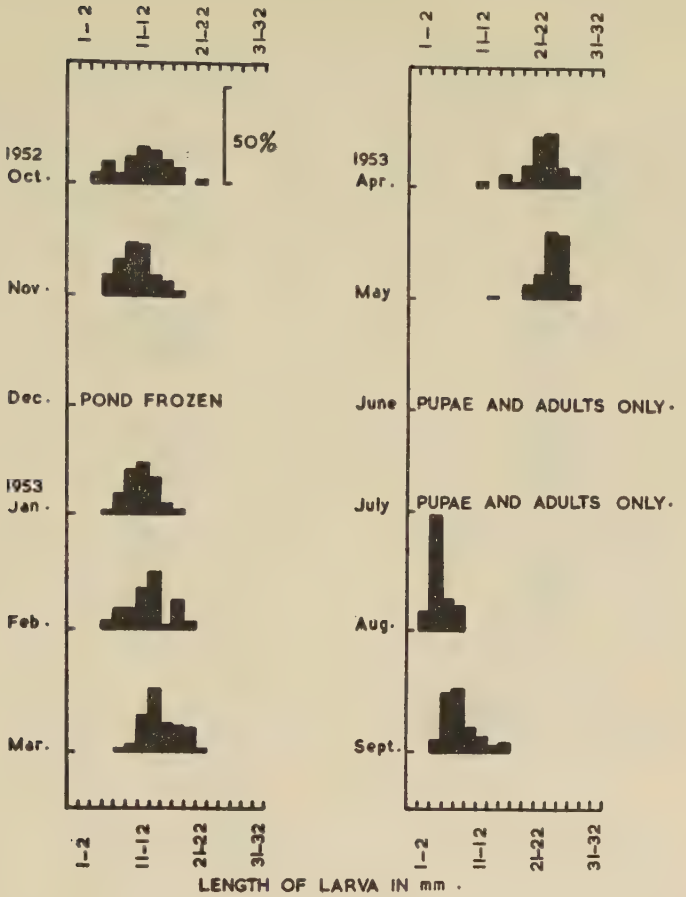


FIG. 1.—The monthly percentage of larvae of *Limnephilus politus* McLachlan in each 2 mm. length class.

and filamentous algae. Between March and April there was a slight rise in the relative increase in size and, at the same time, a marked increase in the number of diatoms and filamentous algae. Between April and May there was a further increase in the rate of growth and also an increase in the number of diatoms and filamentous algae.

Pupae of *M. angustata* were found from early May until late June. In the laboratory, at room temperature, the pupal period lasted about 23 days. Adults were collected from late May until early July and were found resting on the vegetation. There was only one generation a year.

Limnephilus marmoratus Curtis.

The percentage of larvae of *Limnephilus marmoratus* in each 2 mm. length class is shown in figure 3.

The larvae were found in all months of the year except July and August. In December the pond was covered with ice and a small number of larvae was

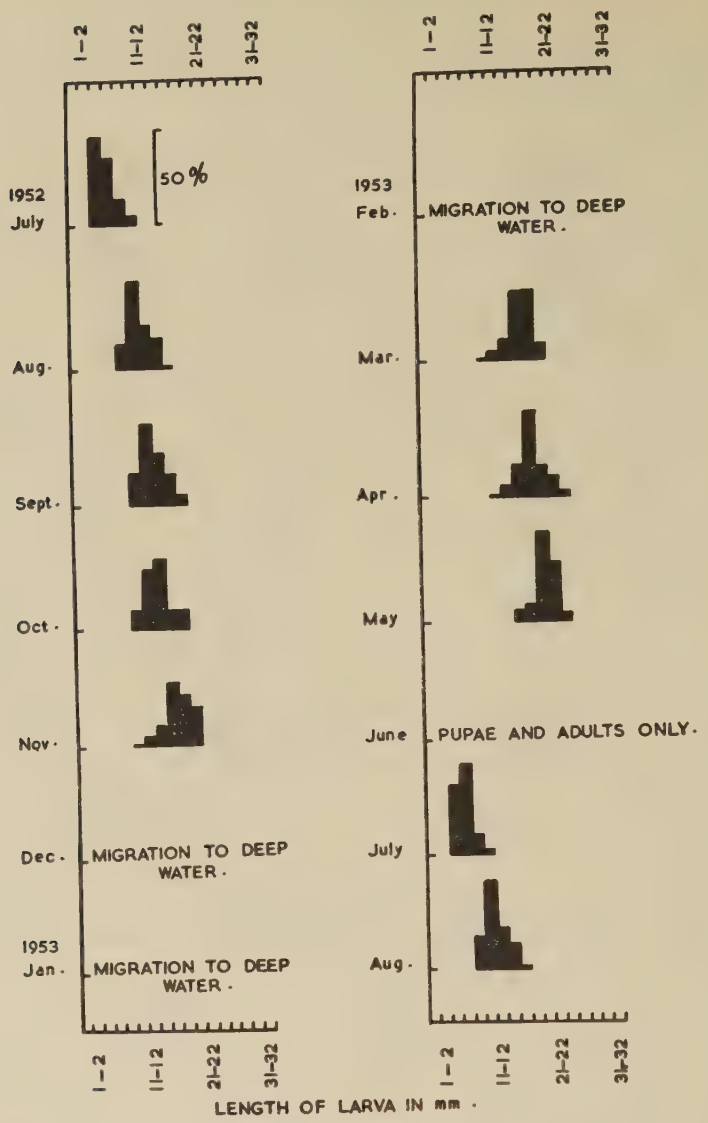


FIG. 2.—The monthly percentage of larvae of *Molanna angustata* Curtis in each 2 mm. length class.

obtained. An examination of the mid-gut, however, showed that there was a considerable reduction in the amount of diatoms, volvocales, chlorococcales, filamentous algae and dead leaves, though the amount of detritus remained more or less constant. No increase in size had taken place between November and January. From January to February there was a considerable increase in size and also a significant increase in the number of diatoms and in the amount of detritus. Between February and June there was a decline in the relative increase in size and also a drop in the amount of food present in the mid-gut.

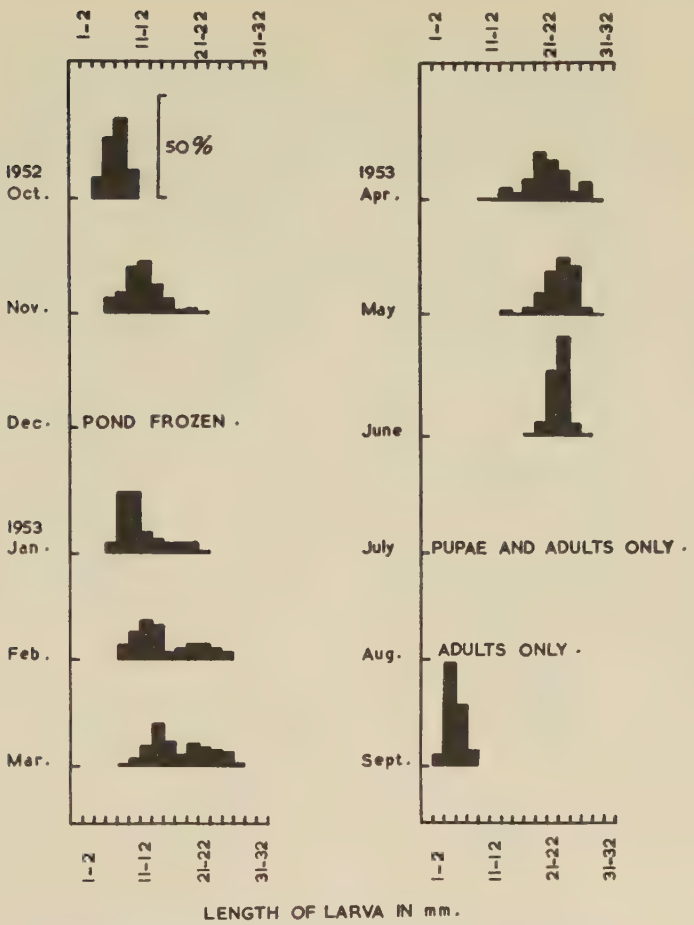


FIG. 3.—The monthly percentage of larvae of *Limnephilus marmoratus* Curtis in each 2 mm. length class.

The larvae grew mainly from October to November, and in this period there was an increase in the number of diatoms, volvocales, and filamentous algae. The desmids were also plentiful in the mid-gut during this period.

Pupae of *L. marmoratus* occurred together with the larvae in late May and were found until late July. In the laboratory, at room temperature, the pupal period lasted about 18 days. The adults were collected from late June until early August, when they were found resting on the vegetation near the pond and only flew if disturbed. There was only one generation a year.

Anabolia nervosa (Curtis).

The percentage of larvae of *Anabolia nervosa* in each 2 mm. length class is shown in figure 4.

The larvae were found in the pond from early November to early September. No specimens were collected in December, January and February and it appears

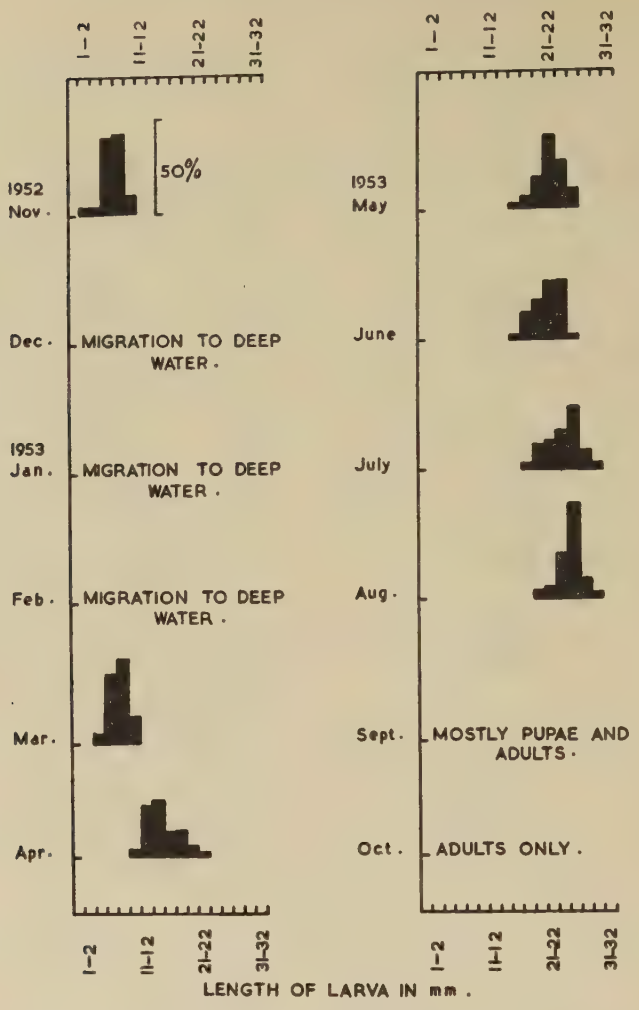


FIG. 4.—The monthly percentage of larvae of *Anabolia nervosa* (Curtis) in each 2 mm. length class.

likely that the larvae migrate into deep water during this period. Between November and March little significant change in the population occurred, showing that there was very little growth in winter. Between March and May the larvae grew rapidly and at the same time a great rise in the number of diatoms and in the amount of detritus in the mid-gut was observed. From May to August there was a decline in the relative increase in size and also a significant reduction in the number of diatoms found in the mid-gut.

Pupae of *A. nervosa* were found from late August until late September. In the laboratory, at room temperature, the pupal period lasted about three weeks. Adults were collected from late September until late October, when they were found resting on the vegetation near the pond and only flew if disturbed. There was only one generation a year.

Discussion.

The rate of growth of the larvae of these four species appears to depend on the combined effect of two factors, namely, food supply and temperature. There is evidence that a substantial increase in the abundance of the food items in the mid-gut was associated with an increase in the rate of growth. When there was a reduction in the amount of food in the mid-gut, a corresponding decline in the rate of growth was observed.

A study of the feeding habits showed that the species examined are primarily detritus feeders. The presence of other food items, such as diatoms, volvocales, chlorococcales and desmids, is subject to considerable variation in amount but whether this is the result of selective action or of temporary increase in the amount of these food items amongst detritus is not known. Similar variations, however, in the amount of volvocales in the mid-gut of *Limnephilus politus* and *Molanna angustata* were to be found simultaneously in both species and, as these two species were collected from the same pond, it is reasonable to suggest that this food item was subject to seasonal variations in abundance. Odd specimens of amphipod Crustacea, isopod Crustacea, trichopteran larvae and Hydroacrina larvae were found in the mid-gut of *Molanna* larvae. It seems likely therefore that *Molanna* larvae can also take animal food when available. No larvae were found with animal food only. The larvae of *Limnephilus marmoratus* and *Anabolia nervosa* occur together in the same habitat and feed essentially on the same food materials. The adults of *Anabolia* emerge in late autumn and the larvae grow mainly in spring and early summer, while the larvae of *L. marmoratus* grow mainly in autumn. Therefore, although the two species occur together, they do not compete for the same food materials.

A difficulty lies in the fact that it is not easy to determine which food items are actually digested and used to nourish the larvae. In the case of diatoms, no empty cases were found in the fore-gut, though these were abundant in the mid-gut. Empty cells of volvocales, chlorococcales, filamentous algae and desmids were also abundant in the mid-gut. It is, therefore, reasonable to assume that these were also digested. Of the detritus and dead leaves little can be said beyond their occurrence, and whether these food items are in fact digested remains an open question for future physiological investigation.

Summary.

(1) The results obtained from the measurements of the lengths of four species of caddis fly larvae each month are described. These species were *Limnephilus politus* McLachlan, *Molanna angustata* Curtis, *Limnephilus marmoratus* Curtis and *Anabolia nervosa* (Curtis).

(2) A method has been devised for making a quantitative study of the composition of the food of the larvae.

(3) The rate of growth varies with the amount of food found in the mid-gut.

(4) The life cycle of all the species lasted one year.

References.

Alm, G., 1926, Beiträge zur Kenntnis der netzspinnenden Trichopterenlarven in Schweden. *Int. Rev. Hydrobiol.* **14** : 233–75.

Badcock, R., 1949, Studies in stream life in tributaries of the Welsh Dee. *J. Anim. Ecol.* **18** : 193–208.

Gätjen, J., 1926, Nahrungsuntersuchungen bei Phryganeidenlarven (*Phryganea* u. *Neuronia*). *Arch. Hydrobiol. Plankt.* **16** : 649–67.

Glasgow, J. P., 1936, The bionomics of *Hydropsyche colonica* McLach. and *H. philpotti* Till. *Proc. R. ent. Soc. Lond.* (A) **11** : 122–8.

Hanna, H. M., 1954, A study of the growth and feeding habits of the larvae of Limnephilidae with special reference to *Limnephilus politus* McLach. and *L. marmoratus* Curt. Univ. Manchester : Unpublished Thesis.

Jones, J. R., 1949, A further ecological study of calcareous streams in the " Black Mountain " district of South Wales. *J. Anim. Ecol.* **18** : 142–59.

—— 1950, A further ecological study of the River Rheidol. The food of common insects of the main streams. *Ibid.* **19** : 159–74.

Khalil, A., 1953, A contribution to the morphology and biology of some British Trichopterous larvae. Univ. Sheffield : Unpublished Thesis.

Lauterborn, R. and Rimsky-Korsakov, 1903, Eine merkwürdige Hydroptiliden Larve (*Ithytrichia lamellaris* Eaton). *Zool. Anz.* **26** : 280–8.

Lloyd, J. T., 1915, Notes on the immature stages of some New York Trichoptera. *J. N.Y. ent. Soc.* **23** : 201–12.

—— 1921, The biology of North American caddis fly larvae. *Bull. Lloyd Lib.* (*Ent.*) **1** : 1–124.

Martynov, A. B., 1930, On the trichopterous fauna of China and Eastern Tibet. *Proc. zool. Soc. Lond.* **1930** : 62–112.

McLachlan, R., 1863, Food of phryganidous larvae. *Zoologist* **21** : 8532–3.

Murphy, H., 1919, Observations on the egg-laying of the caddis fly *Brachycentrus nigrosoma* Banks, and the habits of the young larvae. *J. N.Y. ent. Soc.* **27** : 154–8.

Neave, F., 1933, Ecology of two species of Trichoptera in Lake Winnipeg. *Int. Rev. Hydrobiol.* **29** : 17–28.

Nielsen, A., 1942, Über die Entwicklung und Biologie der Trichopteren mit besonderer Berücksichtigung der Quelltrichopteren Himmerlands. *Arch. Hydrobiol. Plankt.* Suppl. **17** : 255–631.

——1948, Postembryonic development and biology of the Hydroptilidae. A contribution to the phylogeny of the caddis flies and to the question of the origin of case-building. *K. danske Vidensk. Selsk. Skr.* **5** : 1–200.

—— 1950, Notes on the genus *Apatidea* McLachlan with descriptions of two new and possibly endemic species from the springs of Himmerland. *Ent. Med.* **25** : 384–404.

Noyes, A., 1914, The biology of the net-spinning Trichoptera of Cascadilla Creek. *Ann. ent. Soc. Amer.* **7** : 251–72.

Philipson, G. N., 1953, The larva and pupa of *Hydropsyche instabilis* Curtis (Trichoptera : Hydropsychidae). *Proc. R. ent. Soc. Lond.* (A) **28** : 17–22.

—— 1953, The larva and pupa of *Wormaldia subnigra* McLachlan (Trichoptera : Philopotamidae). *Ibid.* **28** : 57–62.

Popowa, A. N., 1927, Über die Ernährung der Trichopterenlarven (*Neureclipsis bimaculata* L., *Hydropsyche ornatula* McLach.). *Z. Wiss. InsektBiol.* **22** : 147–59.

Siltala, A. J., 1907, Über die Nahrung der Trichopteren. *Acta. Soc. Fauna Flora fenn.* **29** (5) : 1–34.

Slack, H. D., 1936, The food of caddis fly larvae. *J. Anim. Ecol.* **5** : 105–15.

Thienemann, A., 1908, Die Fangnetze der Larven von *Philopotamus ludificatus*. *Z. Wiss. InsektBiol.* **4** : 378–80.

Wesenberg-Lund, C. J., 1910, Über die Biologie von *Glyphotaelius punctatolineatus* Retz. nebst Bemerkungen über das freilebende Puppenstadium der Wasserinsekten. *Int. Rev. Hydrobiol.* **3** : 93–114.

—— 1911, Über die Biologie der *Phryganea grandis* und über die Mekanik ihres Gehaüsebaues. *Ibid.* **4** : 65–91.

—— 1911, Biologische Studien über netzspinnende campodeoide Trichopterenlarven. *Ibid. Suppl.* (3) **1** : 1–64.

THE SYSTEMATIC POSITION OF *DICRANOCEPHALUS* HAHN, 1826 AND ITS ALLIES (HEMIPTERA : HETEROPTERA).

By G. G. E. Scudder.

(*Hope Department of Entomology, University Museum, Oxford*).

Introduction.

The tribe Stenocephalini (= Dicranocephalini) has hitherto been regarded as part of the subfamily Alydinae, more recently regarded as a distinct family, the Alydidae, and hemipterists have until now unanimously included it in the superfamily Coreoidea.

Studies on the structure of the egg, male genitalia, female genitalia, salivary glands and other morphological characters of the Stenocephalini[1] indicate that this group shows a different combination of characters from the Coreidae and Lygaeidae. It bridges the gap between these two families, as does the family Largidae.

Nomenclature.

Until recently the genus *Dicranocephalus* has been known under the name *Dicranomerus*. Previous to this the name *Stenocephalus* was cited as the correct generic name, being attributed to Latreille, 1825. Unfortunately Latreille did not use a latinised name and, since Berthold in 1827 was the first to do this, the name *Stenocephalus* must be attributed to him. China (1943) uses the name *Dicranomerus* Hahn, 1826, correctly pointing out that Hahn's genus dated from 1826 and not 1831. Unfortunately in this earlier work, Hahn (1826) used the name *Dicranocephalus* and not *Dicranomerus*. The correct generic citation should, therefore, be *Dicranocephalus* Hahn, 1826.

Although *Stenocephalus* is not a valid name for the genus, the name Stenocephalidae or Stenocephalini is the correct family-group name since Douglas and Scott (1865) were the first authors to use this supra-generic name for the genus.

Egg and Ovary.

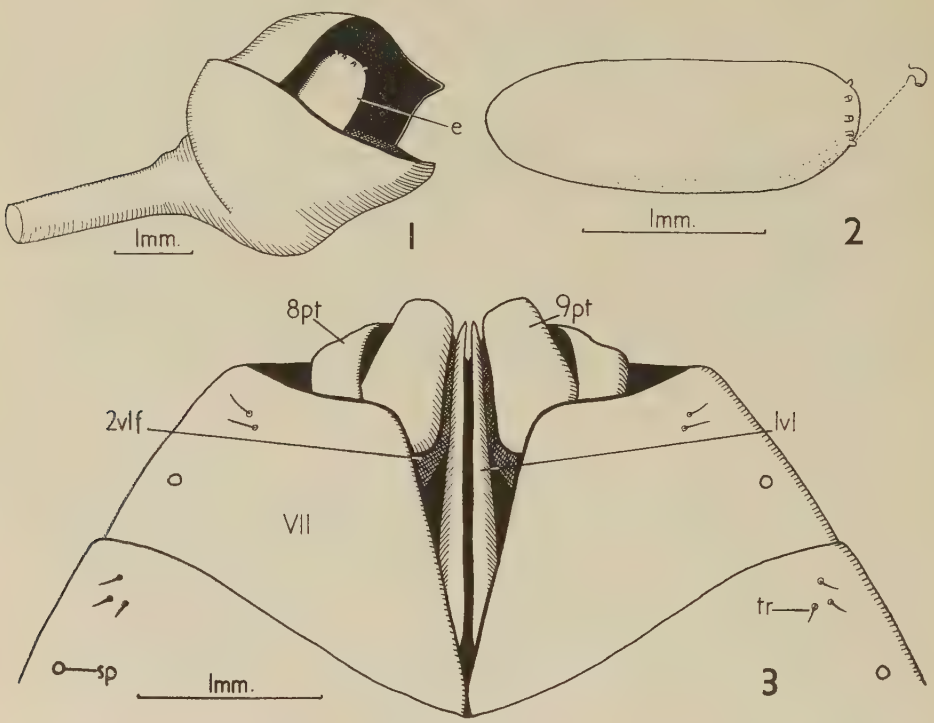
Southwood (1956) noted that the structure of the egg of *Dicranocephalus* was not typical for a Coreid, basing his views on Butler's (1923) brief description. Puchkova (1955) has figured the egg of *Alydus* and *Dicranocephalus*; whilst that of the former is Coreoid in shape and structure, it is clear that the latter is of the Lygaeid type, being oblong in shape with about six[2] micropylar processes at the anterior pole. I have examined the egg of *D. agilis* (Scop.) and find that it has six or seven micropylar processes (figs. 1 and 2). The ovary in *D. agilis* is composed of seven telotrophic ovarioles as in most Heteroptera.

[1] *Dicranocephalus* and *Psotilnus* have been examined.

[2] Puchkova says 4–5 to 9.

Male Genitalia.

Pruthi (1925) showed that the structure of the male genitalia of *Dicranocephalus* (= *Stenocephalus*) resembled neither that of the Pseudophloeinae nor that of the Alydinae, and I am able to confirm this : it is not within the limits of the structure of the Lygaeidae. The parameres are short and twisted (fig. 6) and the pygophore has a median protuberence between the parameres (fig. 5).



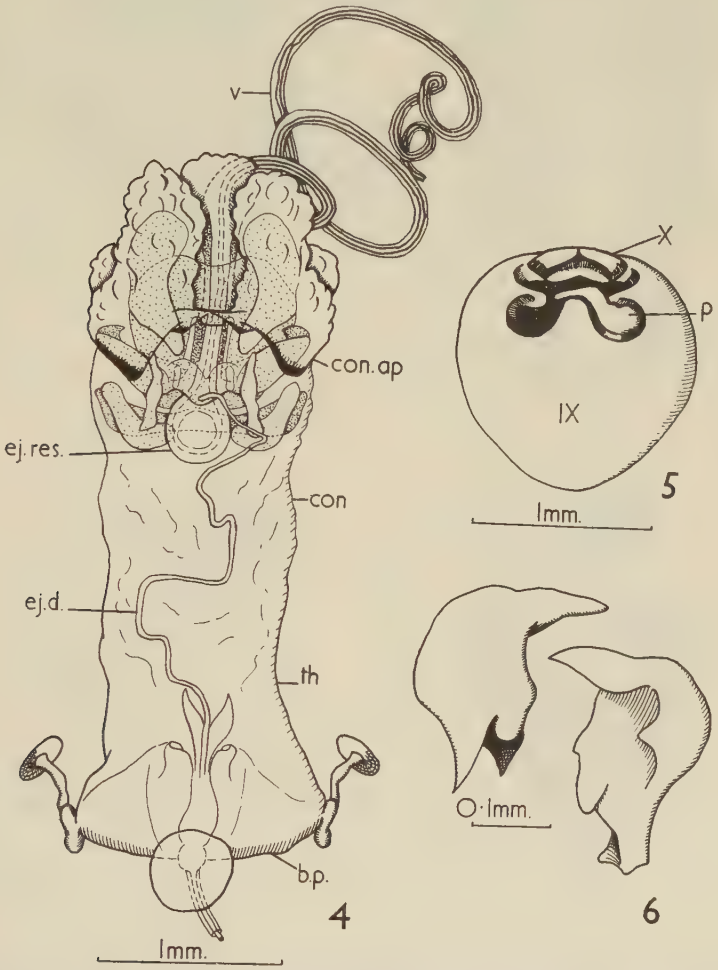
Figs. 1–3.—*Dicranocephalus agilis* (Scopoli). (1) Egg *in situ*. (2) Egg. (3) Ventral view of terminal part of abdomen of female.
For key to lettering see p. 158

The basal plates are stout and the aedeagus (fig. 4) has a wide sclerotic phallosome or theca and a conjunctiva with weakly sclerotised appendages. The vesica is long, flagellum-like and thin, with a thick walled ejaculatory duct within. The ejaculatory reservoir is round and has sclerotisations around it dorsolaterally. Each testis is composed of seven follicles, the usual number in Heteroptera.

Female Genitalia.

The female genitalia of *Dicranocephalus* (figs. 3 and 7–10) are typically Lygaeoid in structure with an elongate ovipositor. The first valvifers (terminology of Snodgrass, 1933) are triangular. The grooved first ramus is long, sclerotised and acutely angled and extends along the dorsal edge of the basal two-thirds of the first valvula. Dorsally it loses its rod-like character and is

flattened, less sclerotised and attached to the base of paratergite IX and to the junction of the first valvifer and paratergite VIII. Paratergite IX at its ventral anterior angle expands to form a broad flattened plate on which the extensor muscles of the valvulae and the retractor muscle of the second valvula are attached (fig. 8). The ventral anterior angle of paratergite IX also forms an apodeme for the posterior dilator muscle of the genital chamber.

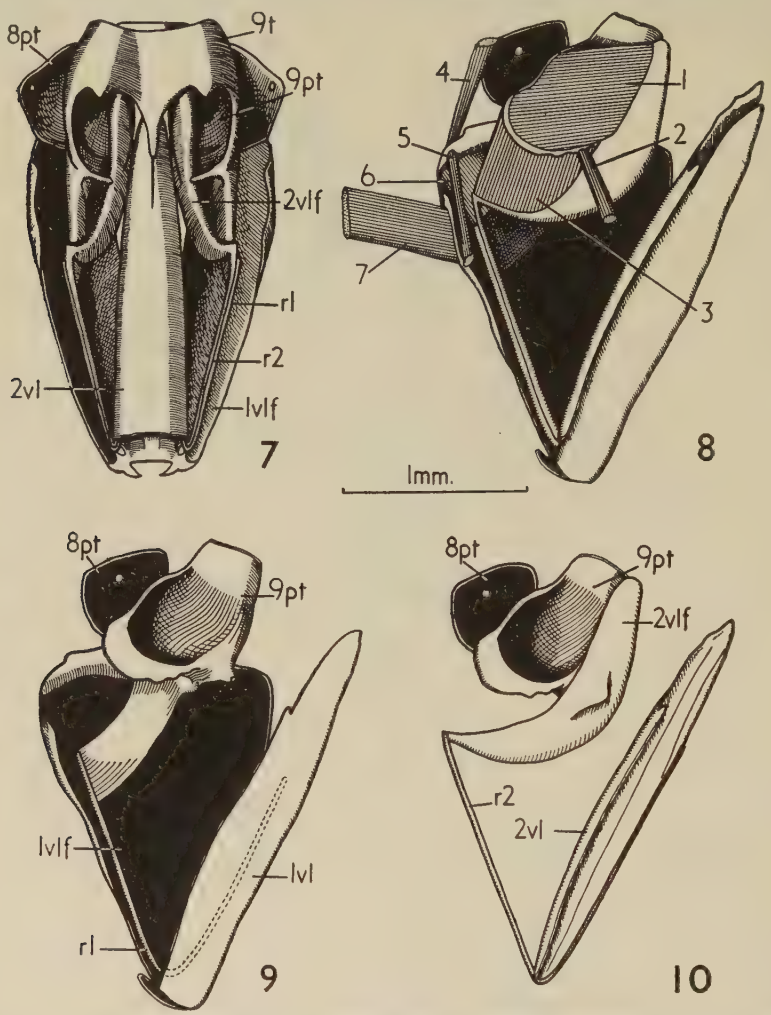


Figs. 4–6.—*D. agilis*, male. (4) Aedeagus. (5) Terminal view of pygophore with left paramere removed. (6) Left paramere, internal and external view.

The second valvifer is crescentic in shape, flattened, and pivots on the ventral posterior angle of paratergite IX. The extensor muscle of the valvulae is attached to the second valvifer posterior to the fulcrum and the retractor muscle of the second valvula anteriorly. To the anterior of the second valvifer is attached also the long, ridged, rod-like, acutely angled second ramus. It extends along the ventral edge of the basal two-thirds of the second valvula.

The ridged second ramus slides on the concave surface of the first ramus during extension and retraction of the ovipositor.

The first and second valvulae are elongate and blade-like, the second pair being fused along the basal two-thirds. The third valvulae are absent.



Figs. 7–10.—*D. agilis*, female. (7) Internal view of female genitalia. (8) Half section of female genitalia showing muscles. (9) First valvifer and associated parts. (10) Second valvifer and associated parts.

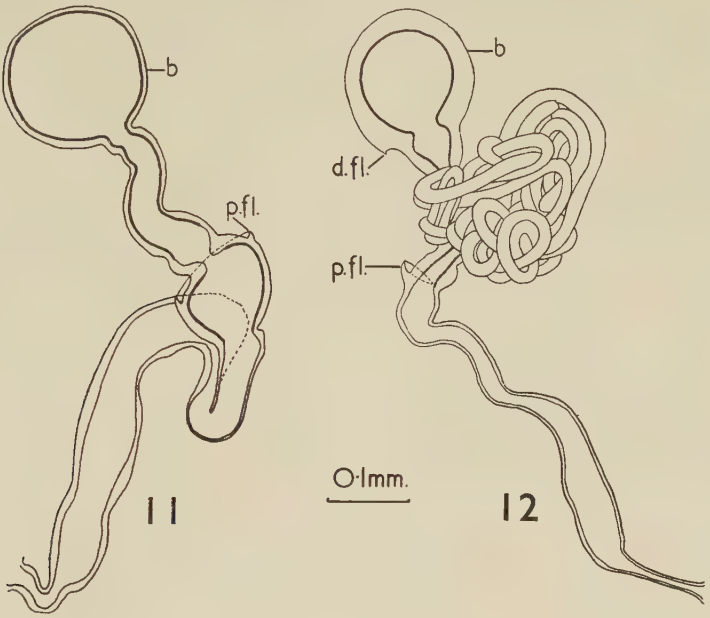
The dorsal anterior part of the first valvifer is strongly sclerotised along the margin where muscles are attached; the tergal muscle of the first valvifer extends from the dorsal anterior margin of the first valvifer to tergum IX. Arising at the same corner of the valvifer is the anterior dilator muscle of the genital chamber. From the inner surface, the retractor muscle of the first valvula extends to the basal part of the expanded portion of the first ramus.

From the dorsal part of the anterior edge, the retractor muscle of the first valvifer extends to the anterior edge of sternum VII.

A pair of ring sclerites is present dorsally in the posterior wall of the genital chamber.

Spermatheca.

The spermatheca enters the genital chamber dorsally, medially and just anterior to the ring sclerites. In *Dicranocephalus* there are two distinct types of spermatheca. In type I (fig. 11) there is a spherical apical bulb with a thick,



Figs. 11–12.—Spermathecae. (11) *D. lateralis*. (12) *D. agilis*.

sclerotic cuticle. The spermathecal duct is composed of two main regions, distally a narrow part with a swollen proximal portion and sclerotised cuticle, proximally a wider part with a thicker, very weakly sclerotised wall. The distal portion of the proximal part of the duct has a very thin wall and the portion of the distal part of the duct before the swelling is thick, but relatively unsclerotised. The swollen portion of the distal part has an annular flange ; the proximal flange and muscles pass from this to the distal flange at the base of the apical spermathecal bulb. The type II spermatheca (fig. 12) is more elaborate, but has a similar sclerotised apical bulb and the spermathecal duct divisible into a distal sclerotised and a proximal weakly sclerotised part. The distal part is tightly and irregularly coiled and the distal and proximal pump flanges are both reduced, being developed to one side only.

Abdomen.

The abdomen of the Stenocephalini is broad and elongate, with seven visible pregenital terga and six visible pregenital sterna. The first sternum is not

visible because it is thrust into the thorax by the consolidation of the pterothorax and the anterior part of the abdomen. Tergum VIII has two anterolateral apodemes, and tergum IX is similarly produced in the mid-line as an apodeme. The dorsal sutures are slightly produced posteriorly at the hind margins of terga IV and V, where the ostioles of the two dorsal abdominal glands are located. A connexivum is present dorsally and is fused with tergum VII. The ventral sutures are straight and sternum VII is cleft to the base in the female. All the abdominal spiracles are situated ventrally towards the lateral margin of the sterna. Ventral abdominal trichobothria are present, three pairs medially on sterna III and IV, three pairs laterally in the form of a triangle to the posterior of the spiracles in the outer thirds of sterna V and VI and two pairs on sternum VII, also in the outer third and posterior to the spiracle.

Salivary Glands.

There are in *Dicranocephalus* (fig. 13), as in all terrestrial Heteroptera so far examined, two pairs of salivary glands. The principal one, which is situated in the thorax, is four-lobed and the principal salivary duct is almost straight. The accessory salivary duct runs posteriorly after first looping into the abdomen. It is long and slightly coiled and is slightly swollen mid-way along its length. Terminally it is elongately swollen in the region of the accessory salivary gland.

Discussion on the Male Genitalia.

Pruthi (1925) showed that in the male genitalia of Coreidae and Lygaeidae, the flattened nature of the basal plates and the general outline of the ejaculatory reservoir related the two families. He stated, however, that Coreidae could be clearly distinguished from Lygaeidae by the possession of conjunctival appendages. He noted that in *Dicranocephalus* the conjunctiva was ornamented with " indistinct thickenings in ventral region, otherwise without any appendages ". He also noted the long flagellum-like vesica.

I have been able to erect the aedeagus of *D. agilis* by manipulation in acetic acid of genitalia previously treated with potassium hydroxide solution. The expanded condition was also obtained by rapidly cooling copulating pairs in a refrigerator. The insects remained *in copulo* but inactive and were then killed and dissected. The aedeagus was dissected from the female complex and then treated with potassium hydroxide solution and acetic acid. Pruthi's figure is of an unexpanded aedeagus and he concluded that it was without conjunctival appendages. These appendages are present, as is clearly seen in figure 4. Whilst this would indicate it to be a Coreid, the nature of the vesica excludes it from this family.

Discussion on the Female Genitalia.

In the Lygaeidae the ovipositor is elongate, laciniate and sclerotised and its form is constant throughout the Lygaeid subfamilies, excluding the Malcinae and Lygaeinae. In the former the female genitalia approach the condition found in the Berytidae. The ovipositor of the Lygaeinae is distinct and shows a reduction of sclerotisation and the formation of isolated sclerites, with associated broadening and folding of the valvulae (Ekblom, 1926 ; Bonhag and Wick, 1953).

The Lygaeidae have the first valvifers triangular or elongate and the sclerotised rami long and acutely angled. The second valvifers are also sclerotised and more or less crescentic in shape. This condition is seen in *Dicranocephalus* and *Psotilnus* and also in the Largidae. In contrast, the Coreidae have the female genitalia more plate-shaped, with the first valvifers more rounded or produced posteriorly and the rami shorter and obliquely angled (Snodgrass, 1933). The second valvifers are often membraneous posteriorly and much broader. The Alydidae possess rami which are characteristically indistinct. The valvulae in Coreoidea are generally membraneous and flap-like. In addition, there is a tendency for the fusion of parts as in the Pentatomoidea, especially the second valvifers, which fuse with each other posteriorly, and ventrally with the second valvulae, as seen in *Rhopalus* and *Alydus*. In both Lygaeoidea and Coreoidea the third valvulae are absent. The Coreoidea have developed sclerotic expansions medially at the base of the second valvifers. These support the genital chamber and are most complex in the Alydidae. Such expansions are absent in Lygaeidae, Largidae and Stenocephalini. In all features the genitalia of *Dicranocephalus* and *Psotilnus* resemble the condition in Lygaeidae and Largidae and are quite unlike Coreoidea.

Discussion on the Spermatheca.

The spermatheca in Coreoidea has been shown by Pendergrast (1957) to be characterised by the absence of a distal pump flange. The muscles of the spermathecal pump are attached to the coiled part of the spermathecal duct. In Lygaeoidea a distal pump flange is present, similar to that found in *Pyrrhocoris* (Ludwig, 1926). In *Dicranocephalus* the spermatheca of type I is typically Lygaeoid with a proximal and a distal pump flange. In the type II spermatheca, however, the distal portion of the spermathecal duct is tightly coiled and one at first assumes that the muscles of the pump attach to this, as in the Coreoidea. Dissections of freshly killed *D. agilis* show that this is not the case. The proximal flange is developed on one side only of the spermathecal duct. The coilings of the distal portion of the duct lie to the other side, and this allows the pump muscles to pass to a distal flange which is likewise present on one side only of the base of the spermathecal bulb. Both types of spermatheca are of the Lygaeoid type.

Discussion on the Abdomen.

The abdominal segmentation in Lygaeoidea and Coreoidea is the same as that in *Dicranocephalus*. The apodemes on terga VIII and IX are not so well developed in Coreoidea and this is associated with the modifications of the genitalia.

The number of dorsal abdominal glands present in the Coreoidea is typically two, located at the posterior margin of terga IV and V. In the Lygaeidae two dorsal abdominal gland openings are present at the posterior of the same terga. In the Rhyparochrominae and Ischnorhynchini some genera have, in addition, a gland opening at the posterior of tergum III. The Cyminae have two glands opening at the posterior of terga III and IV. In Largidae three glands are present. In *Dicranocephalus* two glands are present at the posterior of terga IV and V, as in the Coreoidea and most Lygaeidae.

The dorsal sutures are often produced posteriorly at the dorsal abdominal gland openings. This is especially noticeable in the Coreidae and Alydidae and in some Lygaeid subfamilies. In *Dicranocephalus* and *Psotilnus* they are not produced to the same extent. In Rhopalidae the suture between terga IV and V is produced anteriorly in the mid-line, towards the posterior projection of the preceding suture.

The ventral sutures in the Coreoidea are almost straight, as they are in most Lygaeid subfamilies and Stenocephalini. In most Rhyparochrominae the suture between sterna IV and V is curved anteriorly and does not reach the lateral margin. In Pachygronthinae, Oxycareninae and most genera of Heterogastrinae the female has the posterior ventral sutures curved anteriorly along the ovipositor.

The Coreoidea have the abdominal spiracles all ventral, as have the Lygaeid subfamilies Pachygronthinae, Oxycareninae, Heterogastrinae and Rhyparochrominae (in part). The other subfamilies have the spiracles in various alternative positions. In the Stenocephalini all the abdominal spiracles are ventral.

The ventral abdominal trichobothria on sterna V, VI and VII in the Lygaeidae are in the lateral thirds of the segments, whereas in the Coreoidea the corresponding trichobothria are located in the median thirds *Dicranocephalus* and *Psotilnus* have these structures in the same position as the Lygaeidae. Within the Lygaeidae most subfamilies have the trichobothria on sternum V with one anterior and two posterior to the spiracle. In the Rhyparochrominae the position of these trichobothria is variable. However, on no occasion do all the trichobothria occur in the form of a triangle posterior to the spiracle as in *Dicranocephalus*.

Discussion on the Salivary Glands.

Southwood (1955) has given an account of the salivary gland types in the terrestrial Heteroptera. He finds that there is a difference between the Coreoidea and Lygaeoidea in the structure of the principal salivary gland. The former have this gland four-lobed and the latter three-lobed. The studies of Nuorteva (1956) support these conclusions. In the type of principal salivary gland, *Dicranocephalus* must be placed with the Coreoidea.

Relationships of *Dicranocephalus*.

From the above it can be seen that *Dicranocephalus* falls neither completely in the Lygaeoidea nor in the Coreoidea. It possesses characters of both taxa. The structure of the female genitalia, spermatheca and egg is typical of a Lygaeid, whereas the salivary glands are of the Coreoid type. The male genitalia have characters which on the one hand could place it in the Lygaeidae ; yet, on the other hand, there are characters that could equally place it in the Coreoidea. The position of the abdominal trichobothria in the lateral thirds of sterna V, VI and VII is a Lygaeoid character, yet no Lygaeid examined has the ones on sternum V as does *Dicranocephalus*. In the Coreidae (*Coreus*), however, although the trichobothria are in the median thirds, those on sternum V are in the form of a triangle posterior to the spiracle. In *Alydus*, *Rhopalus* and *Stictopleurus* the corresponding trichobothria, although posterior to the

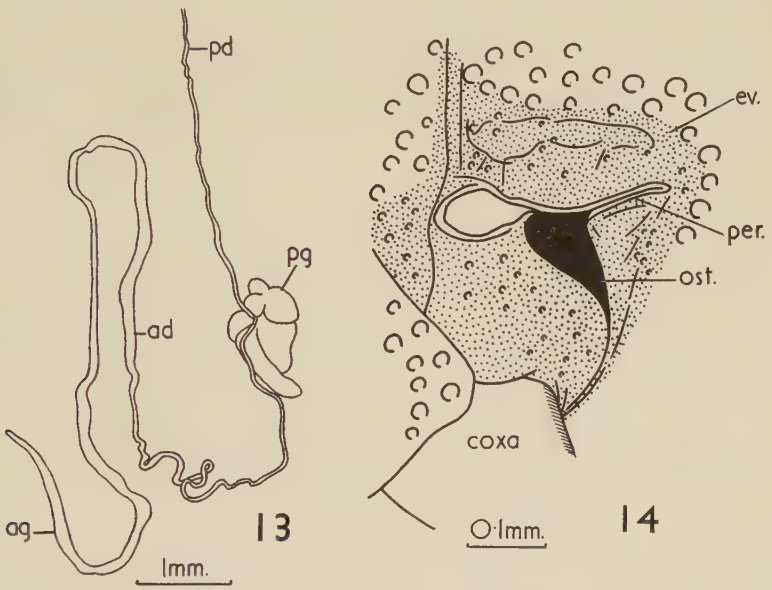
spiracle, are in a linear series transversely and those of the Largidae are in a similar series longitudinally.

The nature of the cleft sternum VII in the female and the position of the spiracles suggest a relationship between *Dicranocephalus* and the Largidae. The position of the spiracles perhaps relate it to some of the Lygaeid subfamilies. However, these groups are all distinct from *Dicranocephalus* on other characters. *Dicranocephalus* and the allied genus *Psotilnus* are considered to represent a new family which lies between the Lygaeidae and Coreidae, although closer to the former and, in many ways, occupying a position similar to Largidae.

Stenocephalidae Douglas and Scott, 1865.

Douglas and Scott, 1865, *Brit. Hem.* **1** : 140.

Head : with ocelli ; eyes remote from pronotum ; antennal tubercle distinct from above ; cephalic trichobothria absent ; paraclypeal lobes produced anteriorly and pointed, projecting well beyond and converging in front of clypeus ; bucculae short and pro-



Figs. 13–14.—*D. agilis.* (13) Salivary glands. (14) Metasternal ostiole region.

jecting. *Metasternal scent gland opening :* clearly visible laterally and with outline as shown in fig. 14. *Fore wing :* membrane with a large and a small basal cell, with numerous radiating and anastomosing veins. *Abdomen :* all spiracles ventral ; connexivum fusing posteriorly with tergum VII ; ventral sutures straight ; sternum VII cleft to base in female ; ventral abdominal trichobothria on sternum V in form of a triangle, all posterior to spiracle and in the outer thirds of the segment. *Male genitalia :* phallosome wide and sclerotised ; conjunctiva with weakly sclerotised appendages ; vesica long and flagellum-like with a thick walled sclerotised ejaculatory duct within. *Spermatheca :* apical bulb spherical and sclerotised ; spermathecal duct of two main regions, distally a slightly narrower duct with sclerotised cuticle, proximally a slightly wider duct with a thick almost unsclerotised wall ; proximal and distal flanges present, latter near the junction of distal and proximal portions of the spermathecal duct.

The Genera of Stenocephalidae.

Stål (1873) recognised two genera within this group, *Dicranocephalus* (= *Stenocephalus*) and *Psotilnus*.

The studies on the spermatheca of *Dicranocephalus* indicate that this genus includes two separate groups. Stål (1873) recognised subgenera in *Dicranocephalus*, but his divisions do not coincide with the grouping based on spermatheca. I have been unable to find any superficial external character to coincide with the division suggested by spermathecae. Under these circumstances, therefore, it is not thought advisable to split the genus. Instead, two species groups are erected. The group with type I spermathecae is designated the "*lateralis* species group" and that with type II spermathecae the "*agilis* species group". The spermatheca of *Psotilnus mucronifer* Stål is the same as that of the *agilis* species group. I have not been able to examine all described species of *Dicranocephalus* but the group assignment of those investigated is as follows :

"*agilis species group*" :

agilis (Scopoli, 1763)
albipes (Fabricius, 1781)
insularis (Dallas, 1852)
lautıceps (Stål, 1859)
marginatus (Ferrari, 1874)
medius (Mulsant and Rey, 1870)
punctıpes (Stål, 1873)
testaceus (Stål, 1859)
tunetanus Horváth, 1887

"*lateralis* species group" :

lateralis Signoret, 1879
pallidus Signoret, 1879.

Geographical Distribution of Stenocephalidae.

Sailer (1952) pointed out that this group was confined to the Old World with the exception of *D. insularis* (Dallas), which occurs in the Galapagos Islands. He said that it would be surprising should this species really belong to the genus *Dicranocephalus*. I have been able to examine the type of *insularis*, a female, which is in the British Museum (Nat. Hist.) and it without doubt belongs to the genus *Dicranocephalus* : the spermatheca is identical with that of *D. agilis*. This confirmation of the generic assignment of the Galapagos species is rather surprising as such an Old World plus Galapagos distribution is unknown elsewhere in the animal kingdom except for one instance in the Mollusca. One would suspect that this family is also present but as yet undiscovered or unrecognised in the New World.

Biological Notes.

The family is associated with Euphorbiaceae. They feed on the ripe seeds and are host specific. The eggs are deposited within the flowers of the plant (fig. 1) (Puchkova, 1955) and evidently not inserted into plant tissue, as suggested by the ovipositor. The larvae are very Coreid-like in appearance and behaviour, especially in the movements of the antennae. In England the overwintered adults oviposit in the spring. Larvae are found throughout the summer and the new adults emerge any time after the third week in August. The period of copulation is prolonged, and a pair kept under observation in the laboratory remained in this condition for more than two weeks.

Acknowledgments.

This work was done in the Hope Department of Entomology, Oxford University, whilst in receipt of a grant from the Department of Scientific and Industrial Research. I am indebted to Dr. A. J. Cain with whom several topics were discussed, Dr. W. E. China, Mr. Dennis Leston and Dr. T. R. E. Southwood for much helpful criticism and for reading the manuscript. I wish to thank the Trustees of the British Museum (Nat. Hist.) for the loan of specimens and permission to examine types, Mr. G. E. Woodroffe for living specimens of *D. agilis* for dissection and Dr. W. J. Le Quesne for help in collecting the same species with me in Devon.

Summary.

(1) *Dicranocephalus* Hahn, 1826 is shown to be the correct designation for the genus previously known under the name *Stenocephalus* Berthold, 1827 or *Dicranomerus* Hahn, 1826.

(2) The genus *Dicranocephalus* and the allied *Psotilnus* have until now been placed in the Coreoidea in the family Alydidae.

(3) A study of the structure of the egg, male genitalia, female genitalia, salivary glands and other morphological characters shows this systematic placing to be incorrect.

(4) The structure of the female genitalia, spermatheca and egg is shown to be typical of a Lygaeid and the salivary glands identical with the Coreoid type. The male genitalia have characters which, on one hand, could place it in Lygaeidae and, on the other hand, in the Coreoidea.

(5) *Dicranocephalus* and *Psotilnus* are considered to represent a new family, Stenocephalidae Douglas and Scott, 1865, which lies between the Lygaeidae and Coreidae, although closer to the former and occupying a position similar to Largidae.

(6) A study of the spermathecae of *Dicranocephalus* indicates that this genus includes two groups with distinct types of spermathecae. Since no external characters have been found to coincide with this division, two species groups are erected.

(7) *D. insularis* is shown to be placed correctly in *Dicranocephalus*.

(8) *Dicranocephalus* is thus shown to have an Old World plus Galapagos Island distribution, a condition unknown elsewhere in the animal kingdom except for one instance in the Mollusca.

References.

Bonhag, P. F. and Wick, J. R., 1953, The functional anatomy of the male and female reproductive systems of the milkweed bug, *Oncopeltus fasciatus* (Dallas) (Heteroptera : Lygaeidae). *J. Morph.* **93** : 177–284.

Butler, E. A., 1923, *A biology of the British Hemiptera-Heteroptera.* London.

China, W. E., 1943, The generic names of the British Hemiptera-Heteroptera, with a check list of the British species. *Generic names of British insects*, Part 8 : 211–342. *R. ent. Soc. Lond.*

Douglas, J. W. and Scott, J., 1865, *The British Hemiptera.* 1. *Hemiptera-Heteroptera.* London.

Ekblom, T., 1926, Morphological and biological studies of the Swedish families of Hemiptera-Heteroptera. Part 1. The families Saldidae, Nabidae, Lygaeidae, Hydrometridae, Veliidae and Gerridae. *Zool. Bidr., Uppsala* **10** : 31–179.

Hahn, C. W., 1826, *Icones ad Monographiam Cimicum.* Nürnberg.

Ludwig, W., 1926, Untersuchungen über den Copulationsapparat der Baumwanzen. *Z. Morph. Ökol. Tiere.* **5** : 291–380.

Nuorteva, P., 1956, Studies on the comparative anatomy of the salivary glands in four families of Heteroptera. *Ann. ent. fenn.* **22** : 45–54.

Pendergrast, J. G., 1957, Studies of the reproductive organs of the Heteroptera, with a consideration of their bearing on classification. *Trans. R. ent. Soc. Lond.* **109** : 1–63.

Pruthi, H. S., 1925, The morphology of the male genitalia in Rhynchota. *Ibid.* **1925** : 127–267.

Puchkova, L. V., 1955, Eggs of Hemiptera-Heteroptera. 1. Coreidae. *Ent. Obozrenie* **34** : 48–55. (In Russian.)

Sailer, R. I., 1952, The identity of *Stenocephalus mexicanus* Ashmead (Hemiptera, Coreidae). *Proc. ent. Soc. Wash.* **54** : 301–3.

Snodgrass, R. E., 1933, Morphology of the insect abdomen. Part II. The genital ducts and the ovipositor. *Smithson. misc. Coll.* **89** (8) : 148 pp.

Southwood, T. R. E., 1955, The morphology of the salivary glands of terrestrial Heteroptera (Geocorisae) and its bearing on classification. *Tijdschr. Ent.* **98** : 77–84.

—— 1956, The structure of the eggs of the terrestrial Heteroptera and its relationship to the classification of the group. *Trans. R. ent. Soc. Lond.* **108** : 163–221.

Stål, C., 1873, Enumeratio Hemipterorum, 3. *K. Vet. Akad. Handl.* **11** (2) : 1–163.

Key to Lettering of Figures.

ad., accessory duct.
ag., accessory gland.
b., spermathecal bulb.
b.p., basal plates.
con., conjunctiva.
con. ap., conjunctival appendages.
d. fl., distal flange.
e., egg.
ej. d., ejaculatory duct.
ej. res., ejaculatory reservoir.
ev., evaporatorium.
ost., ostiole.
p., paramere.
pd., principal duct.
per., peritreme.
p. fl., proximal flange.
pg., principal gland.
r1, *r2*, first and second rami.
sp., spiracle.
th., theca.
tr., trichobothria.
v., vesica.
1vl, *2vl*, first and second valvulae.
1vlf, *2vlf*, first and second valvifers.
8pt, *9pt*, paratergites VIII and IX.
1, extensor of valvulae.
2, posterior dilator of genital chamber.
3, retractor of second valvulae.
4, tergal muscle of first valvifer.
5, anterior dilator of genital chamber.
6, retractor of first valvulae.
7, retractor of first valvifer.
VII, sternum VII.
IX, *X*, segments IX and X.

THE MORPHOLOGY AND ANATOMY OF THE PYGIDIAL GLANDS OF *DIANOUS COERULESCENS* GYLLENHAL (COLEOPTERA : STAPHYLINIDAE).

By M. F. Jenkins.

(*Department of Zoology, University of Bristol*).

I. Introduction.

When Staphylinid beetles are roughly handled, two fleshy protrusible organs are extruded from beneath the last abdominal tergite. These are the pygidial or anal glands, and the behaviour of Staphylinid beetles shows that they function as repellent scent glands. The earliest careful account of such glands was given by Leydig (1859). He identified the evaginated sacs as the reservoirs of the pygidial glands, and when the glands are everted the intima of the reservoirs becomes the external cuticle. Leydig described groups of unicellular gland cells lying around the intima. Each cell possessed a cuticular secretory canal and the canals were gathered into bundles which then penetrated the intima and emptied into the lumen of the gland.

Contrary to this account, Bordas (1899) described for *Ocypus olens* Müll. a glandular apparatus with a group of secretory cells, a long cylindrical collecting canal, a round muscular reservoir, and a very fine excretory tube. Such description accords well with the arrangement of anal or pygidial glands found in some Carabidae, but nothing like this is actually to be found in *Ocypus*, nor is it to be expected in the Staphylinidae where evagination of the pygidial glands is a characteristic reaction.

Apart from the early account by Leydig, the only other important descriptions are those of Dierckx (1899, 1901) who used the largest Staphylinids : *Ocypus olens* Müll., *Staphylinus caesareus* Cederh., and *Ontholestes tessellatus* Geoffr. His account confirms that of Leydig. In *S. caesareus* the gland is differentiated to form a white external pocket and a darkly pigmented inner portion. Secretory cells are restricted to a part of the inner pigmented pocket. Retractor muscles are inserted in both pockets. Evagination of the glands results from an increase of the fluid pressure within the haemocoele consequent upon the curvature and telescoping of the abdomen characteristic of the defence attitude. Normally only the outer sac is everted, and emergence of the inner part of the gland occurs only when a great external pressure is applied which ruptures the attachment of the retractor muscles to the cuticle. Little is known of the nature of the secretion, although it is evidently used for defence in Staphylinids generally, and, as first recorded by Billard and Bruyant (1905), the pygidial gland secretion is employed by some Steninae for lowering the surface tension of water so that they can skim over a water surface.

The anatomy of the pygidial glands has been studied in *Dianous coerulescens* Gyll., and an account for that species serves also for the marsh-living species of *Stenus* which have also been examined.

PROC. R. ENT. SOC. LOND. (A) 32. PTS. 10–12. (DECEMBER, 1957).

II. Material and Methods.

Dianous and species of *Stenus* may be found throughout the year on moss growing near waterfalls and about the banks of quick flowing streams. Attempts were made to cut sections of whole beetles in order to study the anatomy of the anal glands as they lie in their natural position within the beetle. Diaphenol effectively softened the heavy cuticle but also macerated the underlying tissues. No other satisfactory method was found which both softened the cuticle and preserved the structure of the underlying cells. Double embedding techniques also failed to provide satisfactory preparations and such material could only be cut using celloidin techniques. These sections supplemented information gained by dissections. Glands were also dissected out and satisfactorily sectioned after paraffin embedding, but the most useful preparations were made from newly emerged and unhardened adults which were embedded in paraffin wax containing 5 per cent. diethylene–glycol–distearate. Sections were cut at six microns using a rocking microtome. Material was fixed with Bouin's fluid, with Carnoy, Zenker, Susa, and Flemming's fluid without acetic acid. The last gave the best cytological fixation. Sections were stained with Heidenhain's iron haematoxylin with or without an eosin counterstain. No especial study was made of the origin of the secretion.

III. Morphology and Anatomy of the Anal Glands.

The paired pygidial glands lie laterad from the rectum and dorsal to the aedeagus in the male or the vagina in the female (figs. 1–3). In *Dianous* the glands stretch through four abdominal segments. In dissections, where the ninth abdominal segment lies in its natural position within the eighth segment, they appear to reach as far forward as the posterior margin of the fifth abdominal segment. In freshly dissected beetles the glands appear as translucent, shining, secretion-filled sacs showing no surface folds. In freshly fixed material the secretory cells become opaque and may be pulled as a cap from around the membrane of the inner end of the gland. The gland membrane itself appears to be an invagination of the pleurae of the last two abdominal segments. Both glands are connected by the pleural membrane (fig. 2), work in unison, and are everted simultaneously.

The gland membrane is insoluble in cold concentrated sulphuric acid, and in the chitin tests described by Campbell (1929) positive indication was given of chitosan sulphate. The red-violet colour characteristic of chitin was also given with iodine following the alkali treatment. The epidermis is invaginated together with the pleural membrane and follows its contours in the most external part of the gland, as may be seen in sections.

When living anal glands in insect Ringer are vitally stained with methylene-blue, the stain is taken up well by the secretory cell nuclei. The cytoplasm also takes up the stain to some extent, and the numerous secretory vesicles which may be seen in sectioned material are clearly visible as lightly staining areas in the living gland cells.

Dorsally the gland membrane is continuous with the hypodermal cell layer beneath the tenth tergite. Ventrally the membrane is continuous with the dorsal wall of the aedeagal sac in the male and with the dorsal wall of the

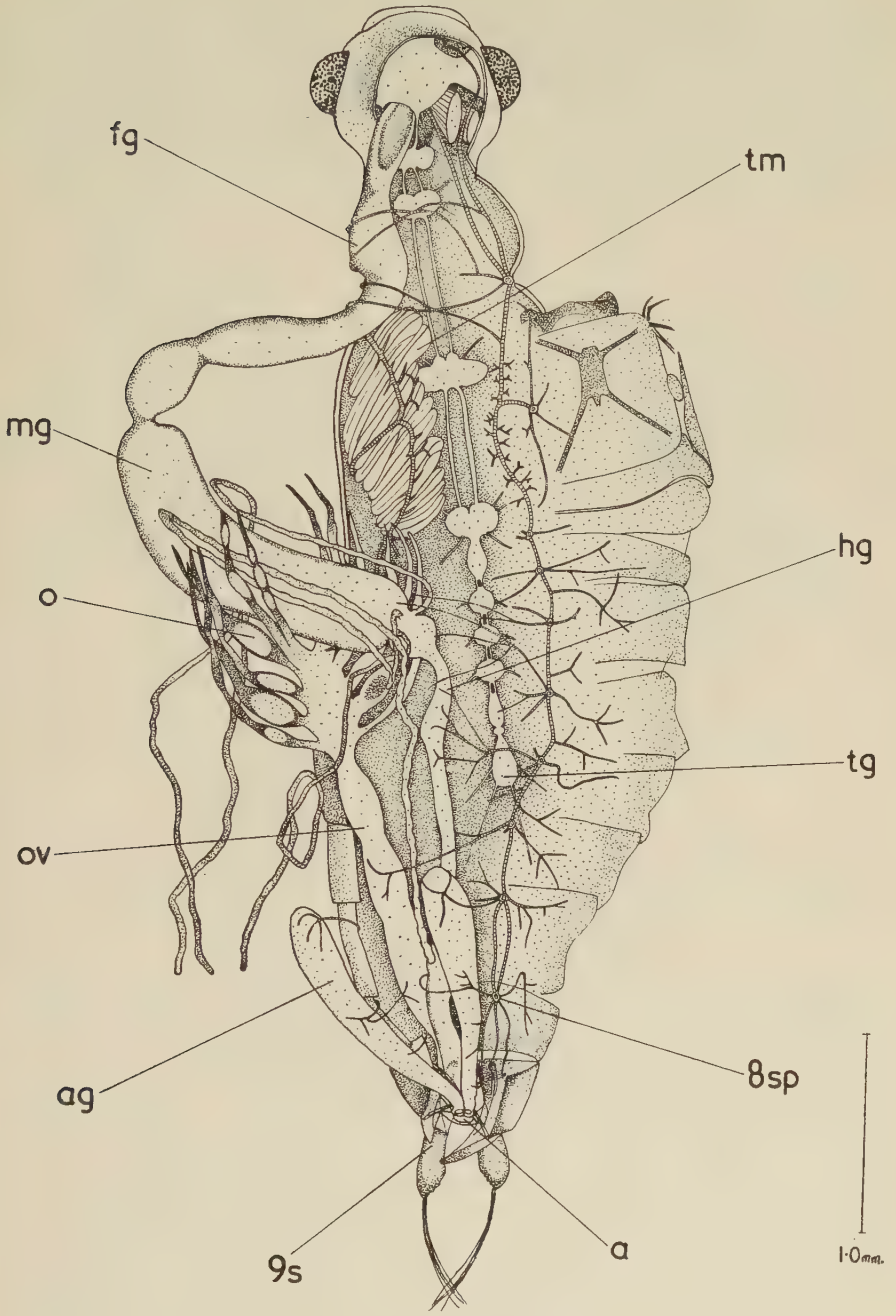


Fig. 1.—General dissection of a female of *Dianous coerulescens* Gyll.
For key to lettering see p. 168

vagina in the female. Medially the gland membrane is continuous with the rectal lining. Laterally it is continuous with the pleural membrane between the ninth tergite and the components of the ninth sternite. The tenth sternite is greatly reduced. In the male (fig. 2) it is represented by the paired, elliptical and lightly sclerotised plates in the roof of the pocket of the aedeagus (Metcalfe, 1932 ; Sharp and Muir, 1912). In the female it is reduced to a small irregular and lightly sclerotised area which rests against the roof of the vagina. The

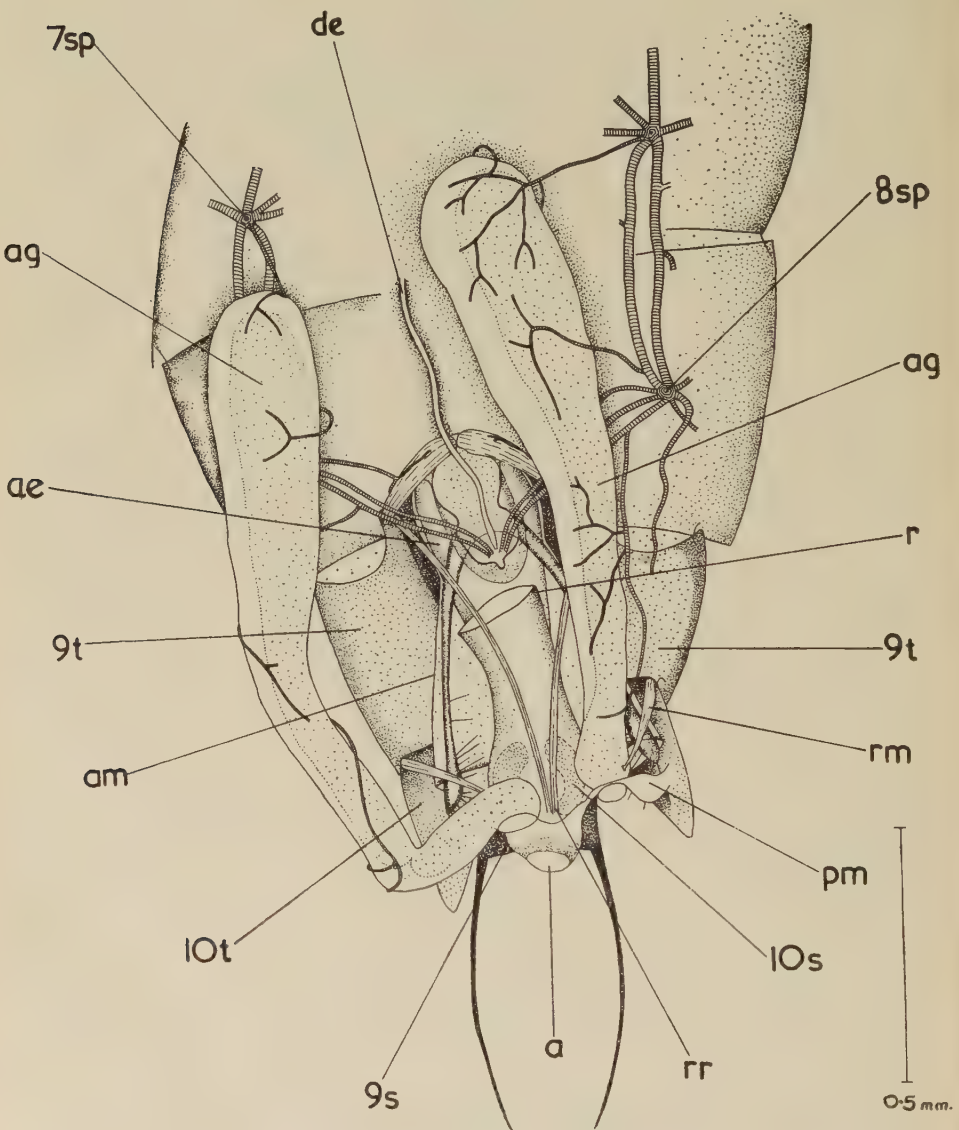


Fig. 2.—Dissection of last abdominal segment of a male of *Dianous coerulescens* Gyll.

reservoirs of the pygidial glands are thus paired invaginations of the continuous pleural membranes of the ninth and tenth abdominal segments.

The junction between the tenth sternite and tergite in the adult is restricted to a membranous connection that is continuous about the rectal opening. The gland membranes thus appear to be invaginations chiefly of the pleural membrane of the penultimate abdominal segment. Morphologically this is the pre-genital or pygidial segment, hence pygidial glands. This designation also

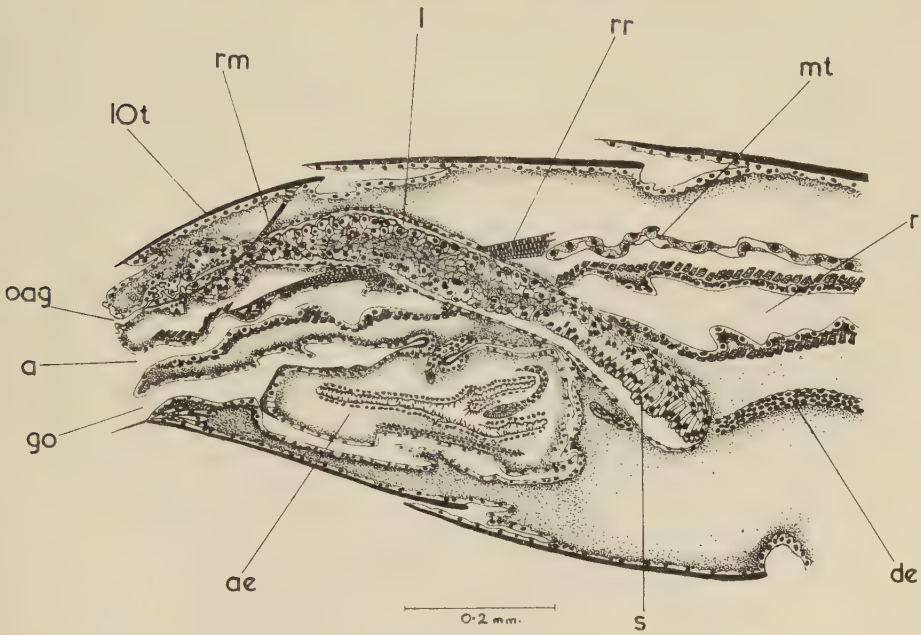


Fig. 3.—Diagrammatic vertical longitudinal section of apical abdominal segments of a male of *Dianous coerulescens* Gyll. The right pygidial gland has been imposed on a section through the mid-line, and the orientation of the secretory cells is indicated.

avoids the difficulties which can arise when giving numbers to the abdominal segments of the Staphylinidae. In this family loss of some anterior sclerites and the telescoping of the posterior ones has led to some confusion in numbering the abdominal segments. In the Steninae the first and second tergites are hidden beneath the elytra and the ninth is ordinarily sheathed within the eighth. The first sternite cannot be seen and may have been incorporated into the coxal cavities (Jeannel and Jarrige, 1949). The second sternite is lost. The true third sternite lies below the first externally visible tergite, and, on superficial examination, may be mistaken for the first abdominal sternite. However, this sternite does not mark the first abdominal segment, and the gland segment is not the seventh. Morphologically, the gland segment is the ninth, *i.e.* the pregenital or pygidial segment, and the glands are precisely described as pygidial glands.

The membranes appear to be everted by increase in blood pressure and to be retracted by the combined action of a muscle inserted on the dorsal wall of

the rectum and a smaller muscle inserted on the gland membrane near its normal opening (figs. 2–3). The rectal muscle originates from the anterior lateral angle of the ninth tergite and the gland muscle from a similar position on the tenth tergite. There is no large muscle running to the posterior or inner part of the gland as described for the larger Staphylinids, and it seems that the gland is held in position to some extent by its tracheal supply which comes from the spiracles of the seventh and eighth abdominal segments. In normal

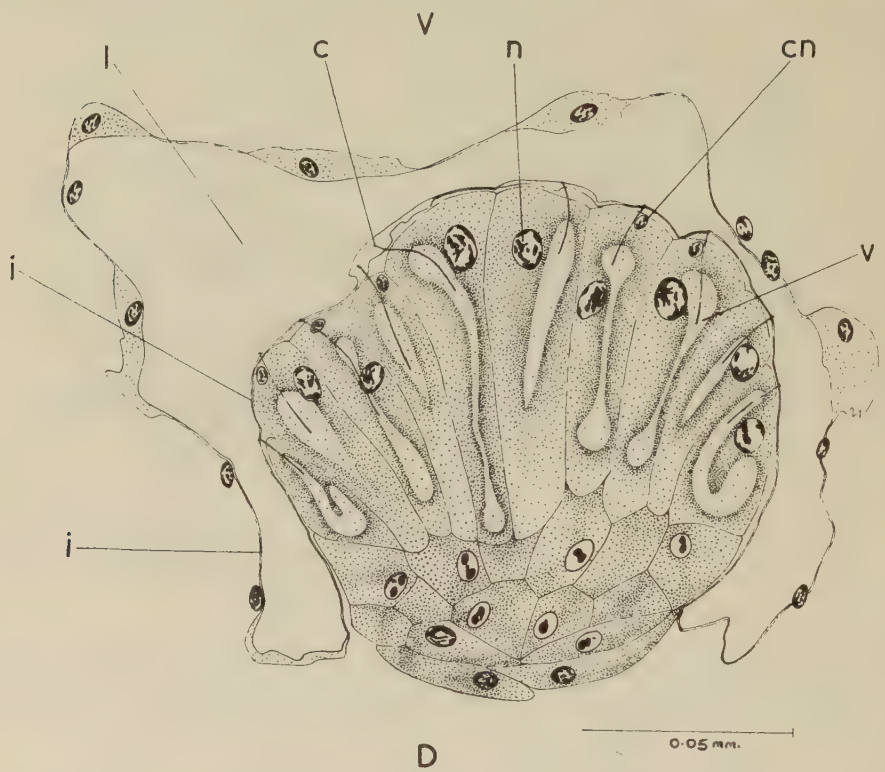


Fig. 4.—Transverse section of the innermost part of a pygidial gland of *Dianous coerulescens* Gyll.

extrusion of the gland, the secretory cells are always bathed in blood and are never exposed to the air.

The secretory cells are distributed throughout the length of the gland, and most of them are specialised as compared with the secretory cells previously described from Staphylinid pygidial glands. The most highly developed secretory cells are those found in the innermost part of the gland (figs. 4–5). The cells there measure approximately 70μ by 12μ. They form a closely packed pile, the inclination of which is constantly dorsoventral in sections. The actively secreting cells in this part of the gland show large vesicles of the secretory substance emptying into the lumen of the gland by exceedingly fine chitinous-lined canals. The canals penetrate the membrane singly and a very small

dilation may be seen at their external openings (fig. 4). Each secretory cell contains a rounded well-staining nucleus towards the gland lumen and a much smaller nucleus adjacent to the point at which the canal runs through the membrane into the gland lumen. This second nucleus may perhaps have been concerned with the production of the chitinous-lined canal.

The pile of secretory cells arises from a mass of more regularly shaped cells which possess neither chitinous canals nor secretory vesicles. These cells and

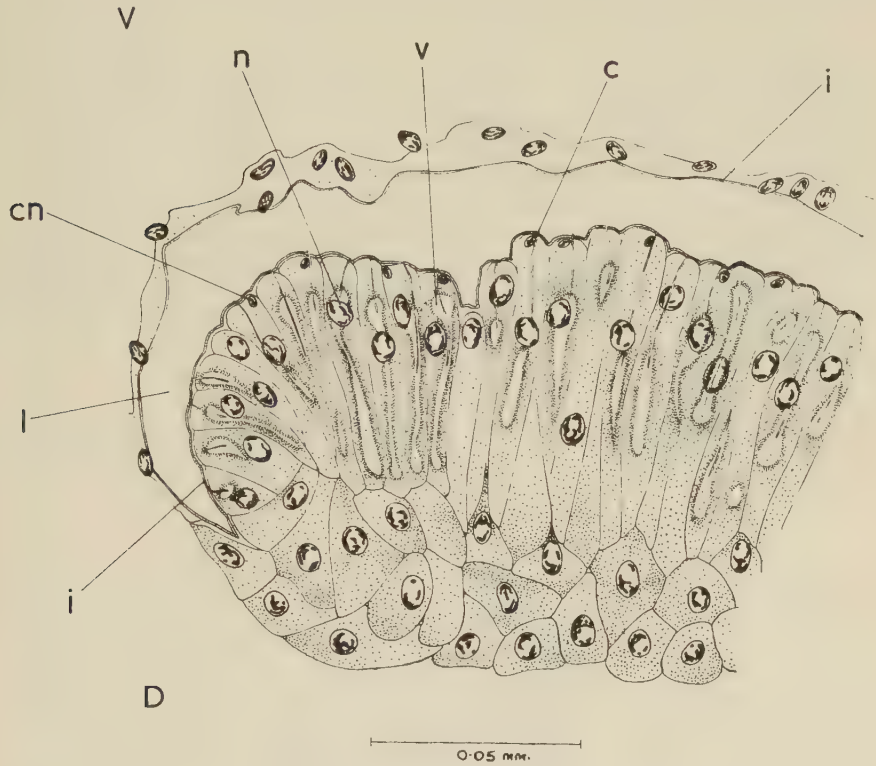


Fig. 5.—Vertical longitudinal section through the innermost part of a pygidial gland of *Dianous coerulescens* Gyll.

the secretory cells are morphologically within the membrane, although appearing in dissections showing exhausted glands to fill the gland lumen, and even in full glands to lie as a pile within it. As previously noted, secretory cells may be pulled away as a cap from the inner end of the gland. That part of the membrane which is not in contact with the specialised secretory cells is nowhere naked but is lined with a single layer of unspecialised cells comparable with those of the epidermis and the cells which line the greater part of the pleural membrane.

Proceeding posteriorly, the inclination of the pile of secretory cells is modified so that half-way along the length of the gland it becomes laterally directed (figs. 6–7). More posteriorly, the common orientation of the secretory cells is lost, they are not as long as cells in the innermost part of the gland, and they

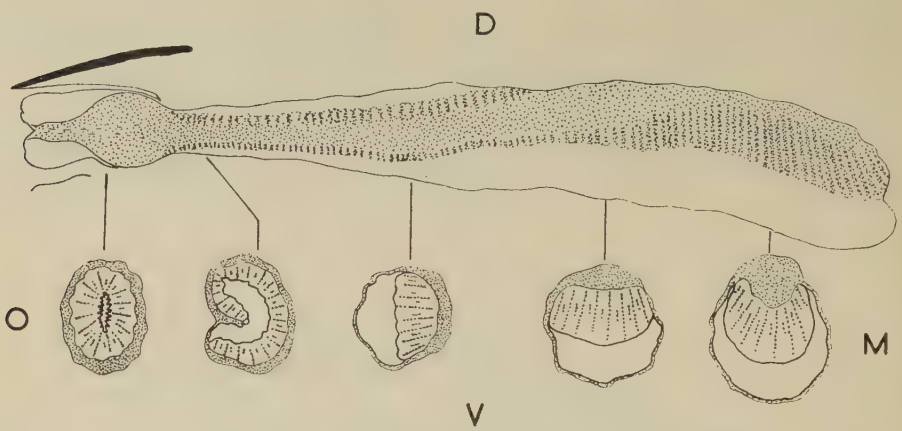


Fig. 6.—Diagram showing orientation of pile of secretory cells along the length of a pygidial gland of *Dianous coerulescens* Gyll. Pygidial gland shown in vertical longitudinal section. Directed stipple parallel to long axes of secretory cells. Random stipple indicates non-secretory cells or secretory cells cut across and not along their long axes.

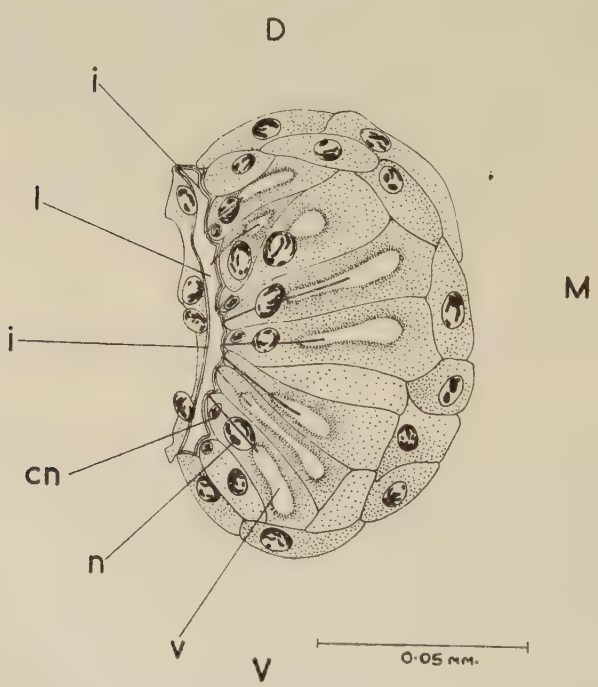


Fig. 7.—Transverse section of a pygidial gland of *Dianous coerulescens* Gyll., cut mid-way along its length.

are distributed all around the gland membrane. Still more posteriorly the secretory cells once again become elongated a little way before the exit of the non-everted gland. Posterior to this region the secretory cells suddenly cease and the unspecialised cells which line the membrane may be seen to be continuous with the epidermal cells.

The nuclei of the secretory cells show no evident changes in size, shape, or staining capacity during secretion. The secretion may thus be a cytoplasmically formed substance or be a product of the cytoplasm and indirectly of the nucleus.

IV. Summary.

The secretion used by the Steninae when lowering the surface tension of water is produced and is stored in paired pygidial glands. In *Dianous coerulescens* Gyll. the musculature of these glands is reduced as compared with that described for the largest Staphylinidae. The secretory cells are mostly elongate, are distributed along the whole length of the cuticular reservoirs, and empty into the gland lumen through fine chitinous-lined canals.

V. Acknowledgment.

My best thanks are due to Dr. H. E. Hinton who suggested the problem to me and assisted me during its progress.

VI. References.

Billard, G. and Bruyant, C., 1905, Sur un mode particulier de locomotion de certains *Stenus*. *C. R. Soc. Biol., Paris*, **59** : 102.

Bordas, L., 1899, Les glandes défensives ou glandes anales des Coléoptères. *Ann. Fac. Sci. Marseille* **9** (5) : 205–49, 2 pls.

Campbell, F. L., 1929, The detection and estimation of insect chitin ; and the interrelation of " chitinisation " to hardness and pigmentation of the cuticula of the American cockroach, *Periplaneta americana* L. *Ann. ent. Soc. Amer.* **22** : 401–26.

Dierckx, F., 1899, Les glandes pygidiennes des Staphylinides et des Cicindélides. *Zool. Anz.* **22** : 311–15, 10 figs.

—— 1901, Les glandes pygidiennes des Coléoptères : Carabides. Paussides. Cicindélides, Staphylinides. *Cellule* **18** : 255–310, 3 pls.

Jeannel, R. and Jarrige, J., 1949, Coléoptères Staphylinides (1ère série). *Arch. Zool. exp. gen.* **86** : 255–392, 105 figs.

Leydig, F., 1859, Zur Anatomie der Insekten. *Arch. Anat. Physiol., Lpz.* **1859** : 33–98 ; 149–78, 3 pls.

Metcalfe, M. E., 1932, The structure and development of the reproductive system in the Coleoptera with notes on its homologies. *Quart. J. micr. Sci.* **75** : 49–129, 4 pls., 49 figs.

Sharp, D. and Muir, F., 1912, The comparative anatomy of the male genital tube in Coleoptera. *Trans. ent. Soc. Lond.* **1912** : 477–642, 65 pls.

KEY TO THE LETTERING OF FIGURES.

a, anus.
ae, aedeagus.
ag, pygidial gland.
am, membrane of pocket of aedeagus.
c, canal (in fig. 4 with minute swelling in cuticle).
cn, canal nucleus.
D, dorsal.
de, ejaculatory duct.
fg, fore gut.
go, opening of pocket of aedeagus.
hg, hind gut.
i, cuticle of gland reservoir.
l, gland lumen.
M, towards the mid-line.
mg, mid-gut.
mt, malpighian tubule.
n, principal nucleus of secretory cells.
o, ovariole.
O, towards the outside.
oag, opening of pygidial gland in rest position.
ov, oviduct.
pm, pleural membrane.
r, rectum.
rm, retractor muscle of pygidial gland.
rr, rectal retractor muscle.
s, pile of elongated secretory cells cut along their long axes.
9*s*, ninth sternite.
10*s*, tenth sternite.
7*sp*, seventh spiracle.
8*sp*, eighth spiracle.
9*t*, ninth tergite.
10*t*, tenth tergite.
tg, terminal ganglion.
tm, thoracic muscle.
v, secretory vesicle.
V, ventral.

Book Notice

Insect Life in the Tropics. By T. W. KIRKPATRICK. 8vo. London (Longmans), 1957. Pp. xiv + 311. text illust. Price 35s.

This book is not primarily addressed to trained entomologists but is intended to give the general reader living in the tropics some idea of the life histories and habits of the insect world around him.

In the first chapter the tropical environment is discussed and then follow chapters on the general structure of insects and on classification designed to render the rest of the work intelligible to the reader with little or no previous knowledge of entomology.

Throughout the work emphasis is laid on types of life history and behaviour rather than on those of specific insects and as far as possible these are based on the author's personal observation.

Chapters are devoted to development, reproduction, locomotion, food and feeding habits, defence and protection, insect architecture and insect communities. A general index completes the work.

THE ABDOMINAL MORPHOLOGY OF A GYNANDROMORPH OF *SCHISTOCERCA PARANENSIS* (BURM.) (ORTHOPTERA : ACRIDIDAE).

By E. Morales Agacino.

(*Madrid*).

[Communicated by Dr. B. P. Uvarov.]

Amongst abundant material of the South American Migratory Locust, *Schistocerca paranensis* (Burm.) *sensu lato*,[3] collected in La Laguna, Departamento de Cortes, Honduras, on 19th November, 1954, by my Guatemalan Assistant in the Comite Internacional de Coordinacion para el Combate de la Langosta en Centroamerica y Mexico (C.I.C.L.A.), Mr. Daniel Soto, I found one gynandromorphic specimen.

I regret the impossibility of describing the internal anatomy of the specimen, because of its poor preservation.

The morphology of the head, thorax and abdomen of the specimen, as well as the respective appendages, is as in a normal male, except in the following parts :

IX–X tergites.—Partly fused as usual. The ninth tergite obtusely angular in the middle of the posterior margin, instead of being concave or convex as it is in the normal male and female, respectively ; this detail is more of the female type. The left half of the posterior margin of the tenth tergite is slightly sinuate, as in the female. The right half has a basal tooth-like projection, as in the male.

Cerci.—The left cercus is conical, compressed, longer than wide, similar to, but slightly larger than in, a normal female. The right cercus is essentially similar to that of a normal male.

Supra-anal plate or epiproct.—The epiproct is of the male type except the left basal quarter which has the external margin not thickened and has no keels in the basal half ; these are the features resembling the female type.

Subanal plates or paraprocts.—The left paraproct is of the female type but of smaller size ; its distal border is almost straight instead of sinuate as in the normal female. The right paraproct is a completely normal male type.

VII sternite.—This does not show any abnormality.

VIII sternite.—Viewed ventrally the right half (*i.e.* the one on the left in this aspect) of this sternite is similar to that of a normal male ; however, the left half (*i.e.* seen on the right), of very similar length, has its external border excised and with a rounded tubercle which corresponds to the characteristic subconiform median process of the female sex.

Ventral, or inferior, ovipositor valve.—This valve, present only on the left side, is a little smaller than normal, and it is more elongated but less thickened.

IX sternite.—This sternite, peculiar to the male sex, is present only on the right side. Externally it is completely normal ; internally it is convex ; the

[3] This is a tentative determination, because the taxonomy of this locust, including intra-specific variation, is not clear at present.

subgenital plate which is its continuation is developed only on the right (left if viewed ventrally); its internal border has a small lobe and forms with the external border a rounded angle; this is clearly different from the angle formed by the two borders in a normal male.

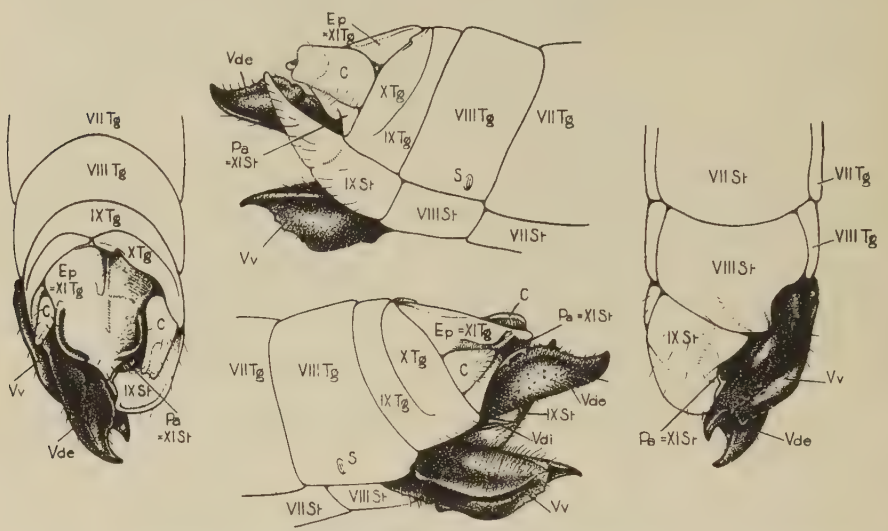


FIG. 1.—Dorsal, two lateral and ventral aspects of abdominal morphology of gynandromorph of *Schistocerca paranensis* (Burm.). *C*, cercus; *S*, spiracle; *Ep*, epiproct; *Pa*, paraproct; *Vdi*, dorsal internal valve of ovipositor; *Vde*, dorsal external valve of ovipositor; *Vv*, ventral valve of ovipositor; *VII–XI St*, seventh to eleventh sternites; *VII–XI Tg*, seventh to eleventh tergites.

Dorsal external or superior ovipositor valve.—This valve is also present only on the left side. It is slightly incurved, being somewhat smaller and less thick than in a normal female.

Dorsal internal, or rudimentary, ovipositor valve.—This shows no evident modification.

LARVAL MORPHOLOGY OF SOME SPECIES OF *PHYTOMYZA* FALLÉN (DIPTERA : AGROMYZIDAE).

By Pamela Allen.

(*Department of Zoology, The University, Glasgow*).

In an earlier paper (Allen, 1957) I discussed the morphology of Agromyzid larvae, previous work in this field, and the need for more detailed descriptions of many species in order to construct a key. An example of the type of key was given, separating some Agromyzids which occur on Umbelliferous plants, and including eight species of the genus *Phytomyza*, which are described more fully in the present paper. A number of features were found common to all and are probably typical of the genus as a whole.

The larval mouthparts, illustrated here for each species, show a similarity of structure. The mandibles each bear two teeth, the right mandible being larger so that the teeth alternate. The teeth are mostly directed ventrally, except in *Phytomyza spondylii* Robineau-Desvoidy. There is only a trace of a suture between the labial sclerite and the paraclypeal phragma. The dorsal angle is about half way along the upper arm of the dorsal process, which is curved at the end ; the lower arm is small. There are foramina in the ventral process.

Sense papillae of the facial mask were extremely difficult to distinguish with any degree of certainty, and are therefore not included in these descriptions. They may show specific differences, but because of this difficulty are not reliable characters to use in a key until a good technique for studying them is developed. Longitudinal sclerites are present in all eight species, but are not very dark. Lateral sclerites, when they occur, are also pale, and anterolaterals are not found at all.

Sixteen sense papillae are usually present on each of the body segments but counts of 15 and 17 are not uncommon. Those of the eighth abdominal

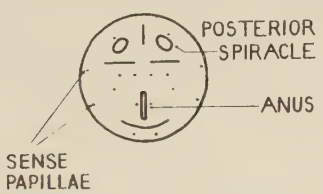


Fig. 1.—Sense papillae of the posterior segment.

segment (fig. 1) form a pattern which is similar in at least seven of the eight species, but *Phytomyza silai* Hering did not display it so clearly.

Emergence from the puparium is by means of a fracture in the first abdominal segment, and a lateral fracture of the thorax region. Mid-dorsal fracture of the thorax does not occur.

The pattern diagrams of the intersegmental tubercle bands and muscle scar bands have been explained in my earlier paper. The striped areas represent tubercle bands of constant occurrence, and the dotted sections those parts where tubercles were found only in some of the specimens examined.

Examination of the features described below for each species reveals sufficient difference to separate the species, with the exception of *Phytomyza anthrisci* Hendel and *P. conopodii* Hering, which seem inseparable on the basis of larval characters.

Phytomyza angelicae Kaltenbach. (Fig. 2).

Puparium dark, deeply ridged, with indentations between the segments; anal lobes present; tubercles irregularly scattered in bands, which may be over 60 per cent. of total segment width measured at the side of the mid-abdominal segments; muscle scars usually more or less rounded. Anterior spiracles T-shaped, with about 10 bulbs (according to de Meijere, 1926, *c.* 12); posterior spiracles oval, with 19–20 bulbs (de Meijere found 20–22). Frontal process absent; lateral sclerites present, though pale.

Phytomyza anthrisci Hendel. (Fig. 3).

Puparium dark, smooth and shiny, without deep indentations between the segments, and with well marked "shoulders" at the anterior end; muscle scars oval, elongated transversely, not anteroposteriorly; tubercles fine, irregularly scattered in bands of up to 40 per cent. of segment width at side of body. Anterior spiracles T-shaped, with 9–13 bulbs (10–12, de Meijere, 1926), posterior spiracles oval, with 14–21 (16–24, de Meijere, 1926 and 1937). Frontal process present; lateral sclerites weak or absent.

Phytomyza conopodii Hering. (Fig. 4).

Puparium dark, smooth and shiny, without indentations; tubercles fine, the bands occupying up to 44 per cent. of segment width at side of abdomen; muscle scars elongate oval. Anterior spiracles T-shaped with *c.* 11 bulbs (de Meijere, 1943, 12–13); posterior spiracles T-shaped or oval with *c.* 18 bulbs (de Meijere, 14–20). Frontal process present; and faint lateral sclerites.

Phytomyza melana Hendel. (Fig. 5).

Puparium dark, smooth, shiny, and without strong intersegmental indentations; muscle scars elongate oval to rounded, and tubercles scattered in bands of up to 46 per cent. of lateral segment width. Anterior spiracles T-shaped or two-horned, with 11–12 bulbs; the posterior spiracles oval with 12–17 bulbs. Frontal process absent; lateral sclerites present but weak.

Phytomyza obscurella Fallén. (Fig. 6).

Puparium dark, smooth, shiny, and without indentations; tubercles rather fine, the bands sometimes over 40 per cent. of lateral segment width. Anterior spiracles T-shaped, with 12–13 bulbs (*c.* 18–20, de Meijere, 1926); posterior spiracles oval or somewhat branched, with 22–29 bulbs (de Meijere, *c.* 26). Frontal process absent, but lateral sclerites present.

Phytomyza silai Hering. (Fig. 7).

Puparium dark, smooth and shiny, without intersegmental grooves; tubercles fairly large and irregularly scattered in bands of up to 45 per cent. of lateral segment width; muscle scars elongate oval. Anterior spiracles T-shaped or branched, with 10–14 bulbs

(de Meijere, 1937, *c.* 12); posterior spiracles oval with 15–20 bulbs (de Meijere, *c.* 20). Pale lateral sclerites and a frontal process present.

Phytomyza spondylii Robineau-Desvoidy. (Fig. 8).

Puparium dark, with intersegmental grooves and numerous ridges; muscle scars fairly short and broad; tubercles irregularly scattered in bands of up to 50 per cent. of segment width. Anterior spiracles T-shaped or two-horned, with 11–15 bulbs (de Meijere, 1926, *c.* 10–14; 1928, 18); posterior spiracles also T-shaped with 19–26 bulbs (de Meijere, 1926, *c.* 16–21; 1928, up to 26). Frontal process absent; lateral sclerites present but weak. Mouthparts of the form described above, but teeth of mandibles situated at right angles to long axis of mandibles, and not pointing downward as in other species.

Phytomyza tordylii Hering. (Fig. 9).

Puparium dark, smooth and shiny, without ridges or indentations; muscle scars elongate oval; tubercles irregularly scattered in bands of up to 44 per cent. of segment width. Anterior spiracles T-shaped with *c.* 15 bulbs (de Meijere, 1937, *c.* 16); posterior spiracles also T-shaped with *c.* 21 bulbs (de Meijere, *c.* 18). Longitudinal and lateral sclerites and also frontal process present.

Summary.

The larval morphology of eight species of the genus *Phytomyza* is described. Features common to all are possibly typical of the genus. All these species can be separated by study of their larval morphology, with the probable exception of *P. anthrisci* Hendel and *P. conopodii* Hering.

References.

Allen, P., 1957, The larval morphology of Agromyzidae (Diptera). *Proc. R. ent. Soc. Lond.* (A) **32** : 59–66.

Frick, K. E., 1952, A generic revision of the family Agromyzidae (Diptera) with a catalogue of New World species. *Univ. Calif. Publ. Ent.* **8** : 339–452.

Hendel, F., 1931–36, Agromyzidae, *in* Lindner, *Flieg. Pal. Reg.* **59**, 570 pp.

Meijere, J. C. H. de, 1925–26, Die Larven der Agromyzinen. *Tijdschr. Ent.* **68** : 195–293; **69** : 227–317.

—— 1928–1943, Ditto. Nachtrag (1), (3), (4), (7) *Ibid.* **71–86**. (1) 1928, **71** : 145–178; (3) 1937, **80** : 167–243; (4) 1938, **81** : 61–161; (7) 1943, **86** : 61–76.

—— 1955, Ditto. General-Register. *Ibid.* **98** : 1–27.

(For figures 2–9 see pages 174–181).

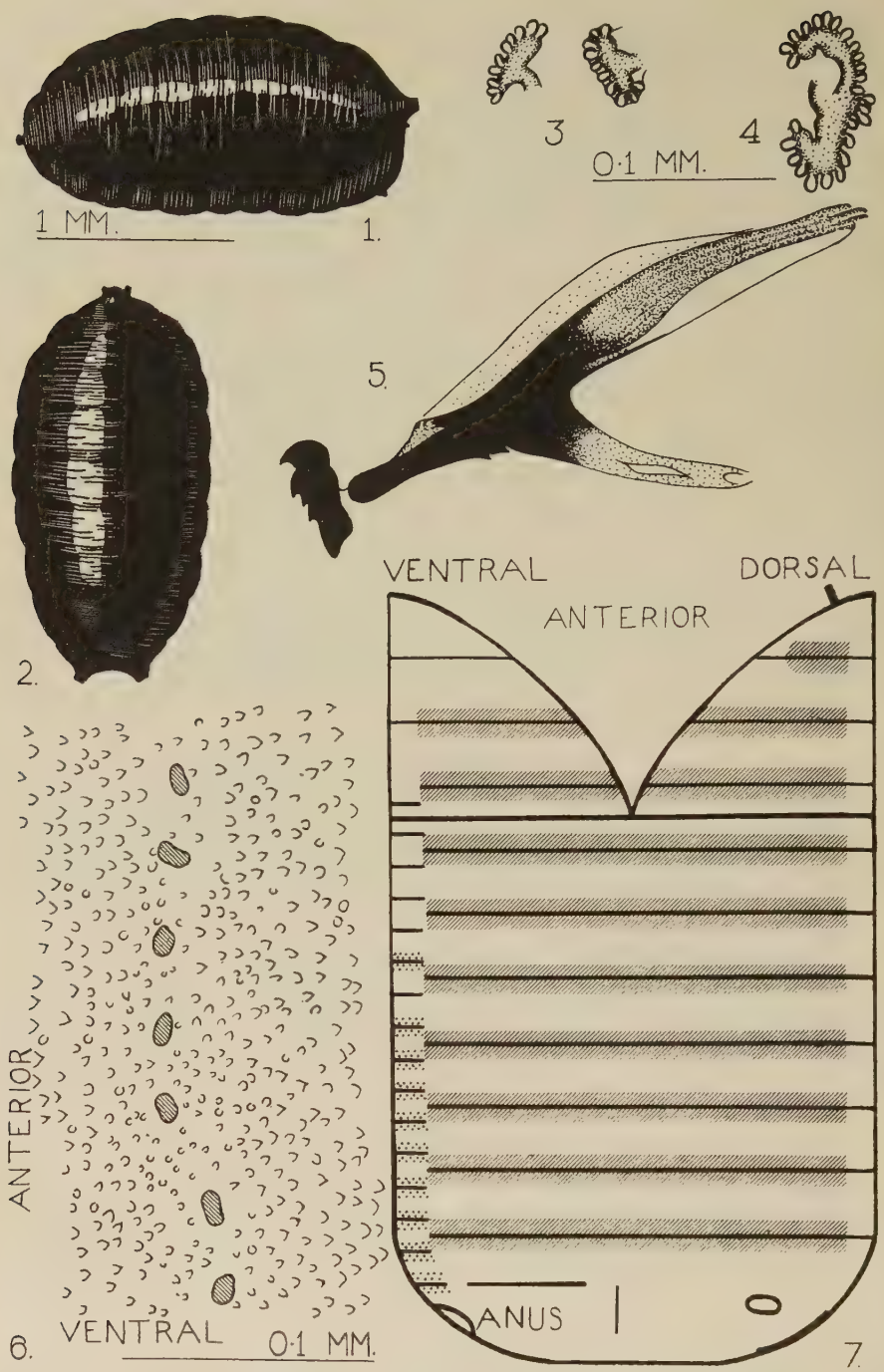


Fig. 2.—*P. angelicae* Kaltenbach. (1) Side view of untreated puparium. (2) Dorsal view of untreated puparium. (3) Anterior spiracles of larva. (4) Posterior spiracle of larva. (5) Larval mouthparts, third instar. (6) Portion of the post-fourth abdominal intersegmental tubercle band at the side of the body, drawn from an acid-treated puparium. (7) Muscle scar and tubercle band pattern.

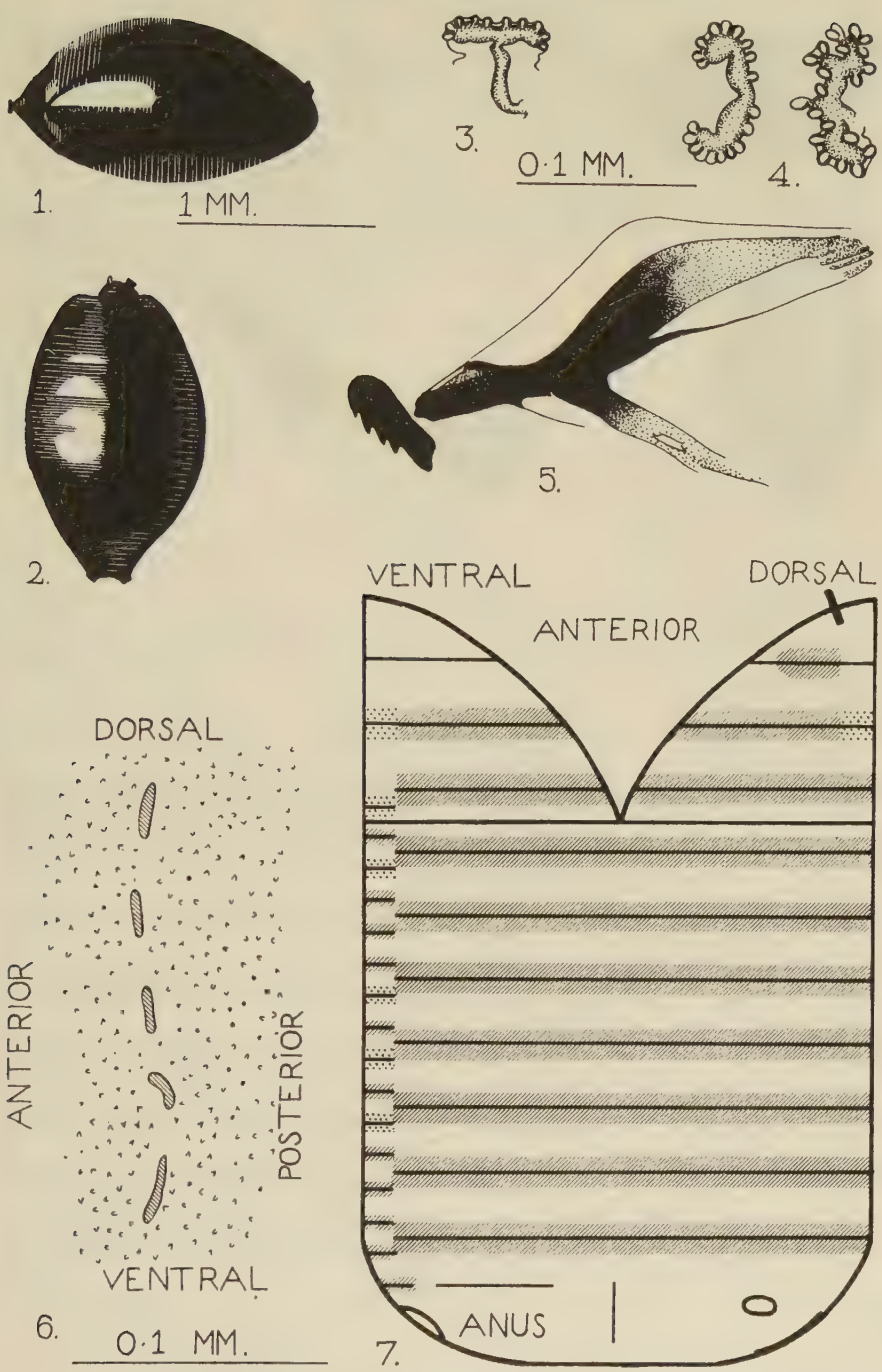


Fig. 3.—*P. anthrisci* Hendel. (1) Side view of puparium. (2) Dorsal view of puparium. (3) Anterior spiracle of larva. (4) Posterior spiracles of larva. (5) Larval mouthparts, third instar. (6) Portion of the post-fourth abdominal tubercle band. (7) Muscle scar and tubercle band pattern.

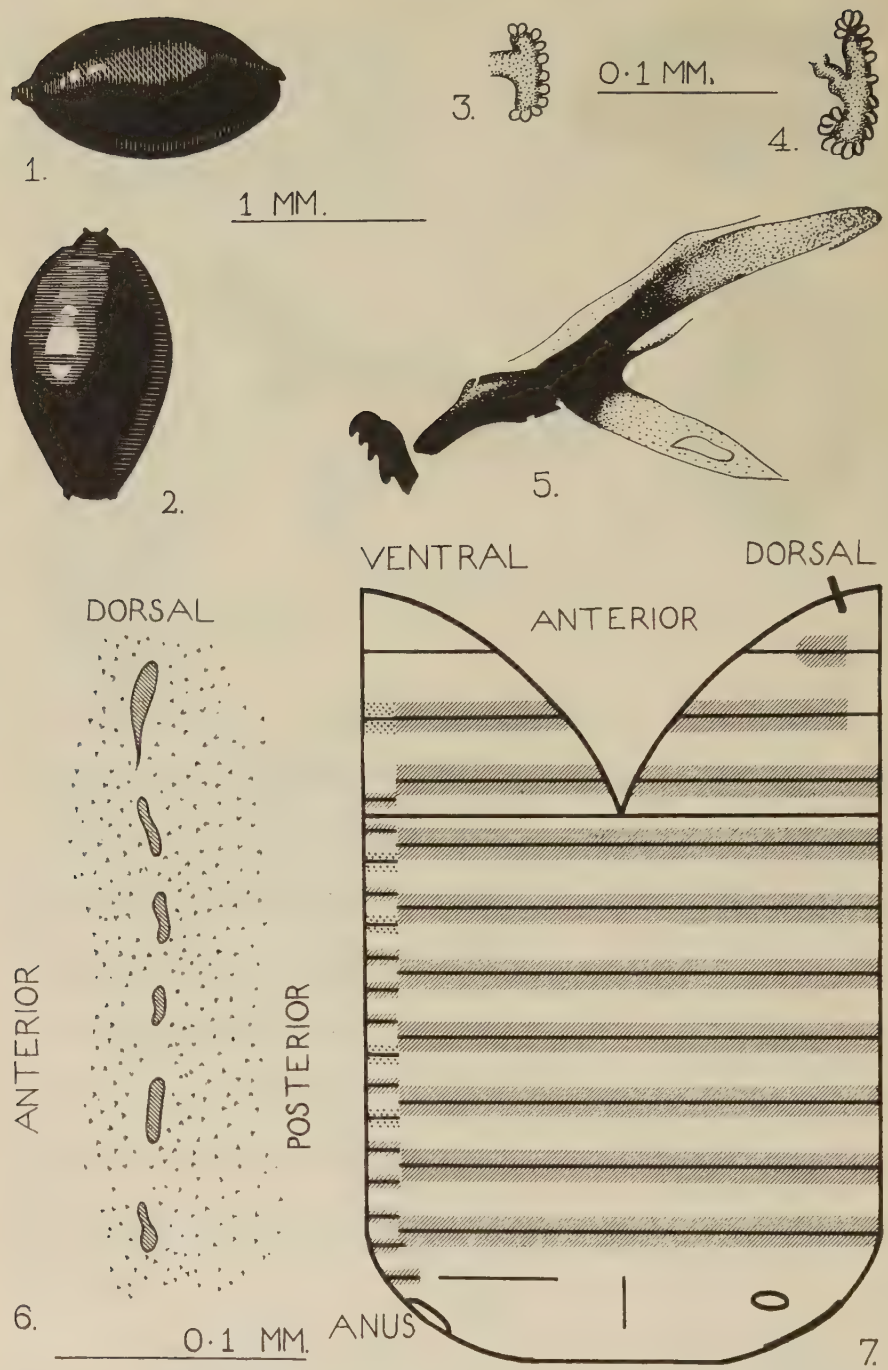


Fig. 4.—*P. conopolii* Hering. (1) Side view of puparium. (2) Dorsal view of puparium. (3) Anterior spiracle of larva. (4) Posterior spiracle of larva. (5) Larval mouth-parts, third instar. (6) Portion of the post-fourth abdominal tubercle band. (7) Muscle scar and tubercle band pattern.

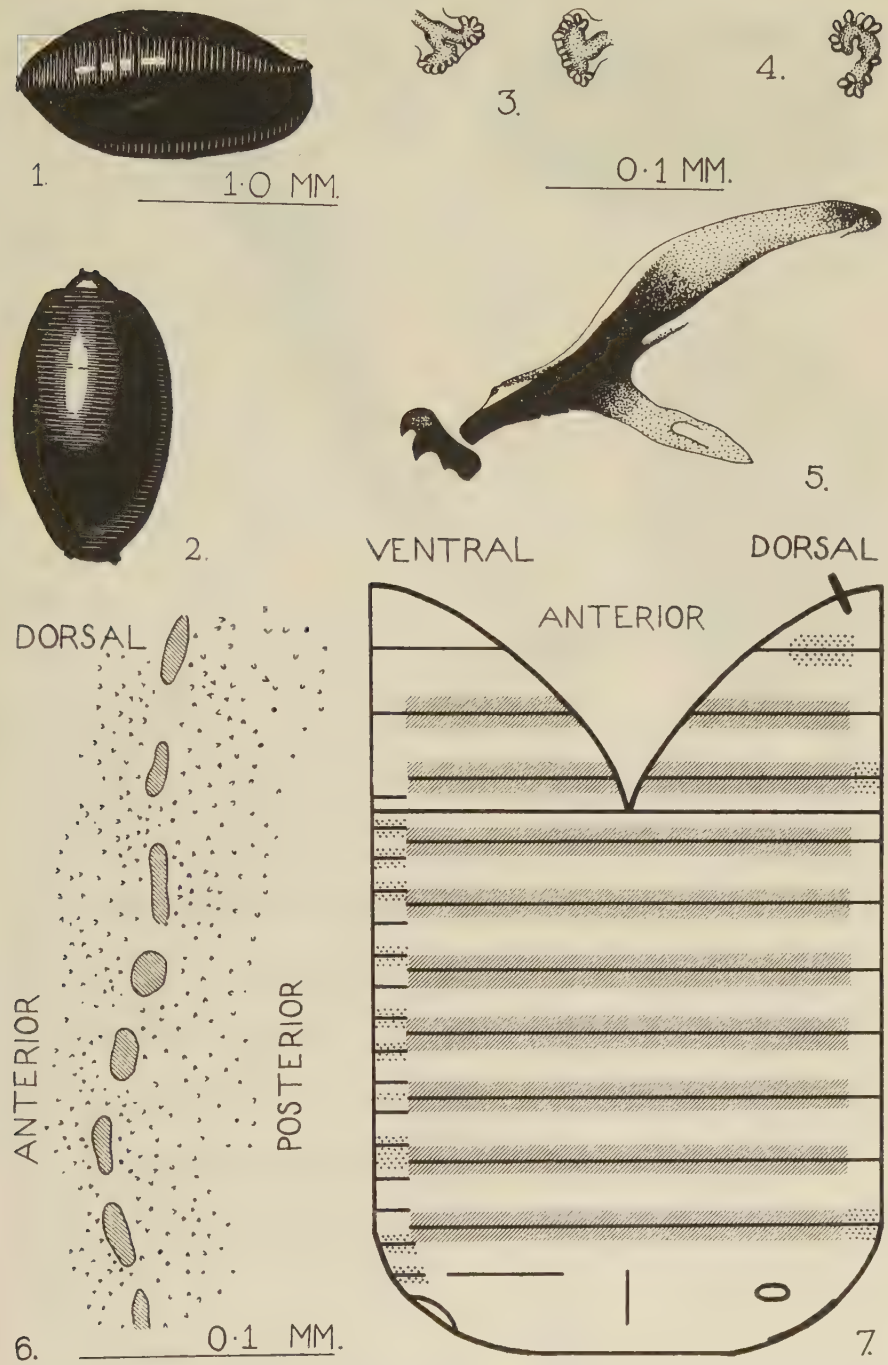


Fig. 5.—*P. melana* Hendel. (1) Side view of puparium. (2) Dorsal view of puparium. (3) Anterior spiracles of larva. (4) Posterior spiracle of larva. (5) Larval mouthparts, third instar. (6) Portion of post-fourth abdominal tubercle band. (7) Muscle scar and tubercle band pattern.

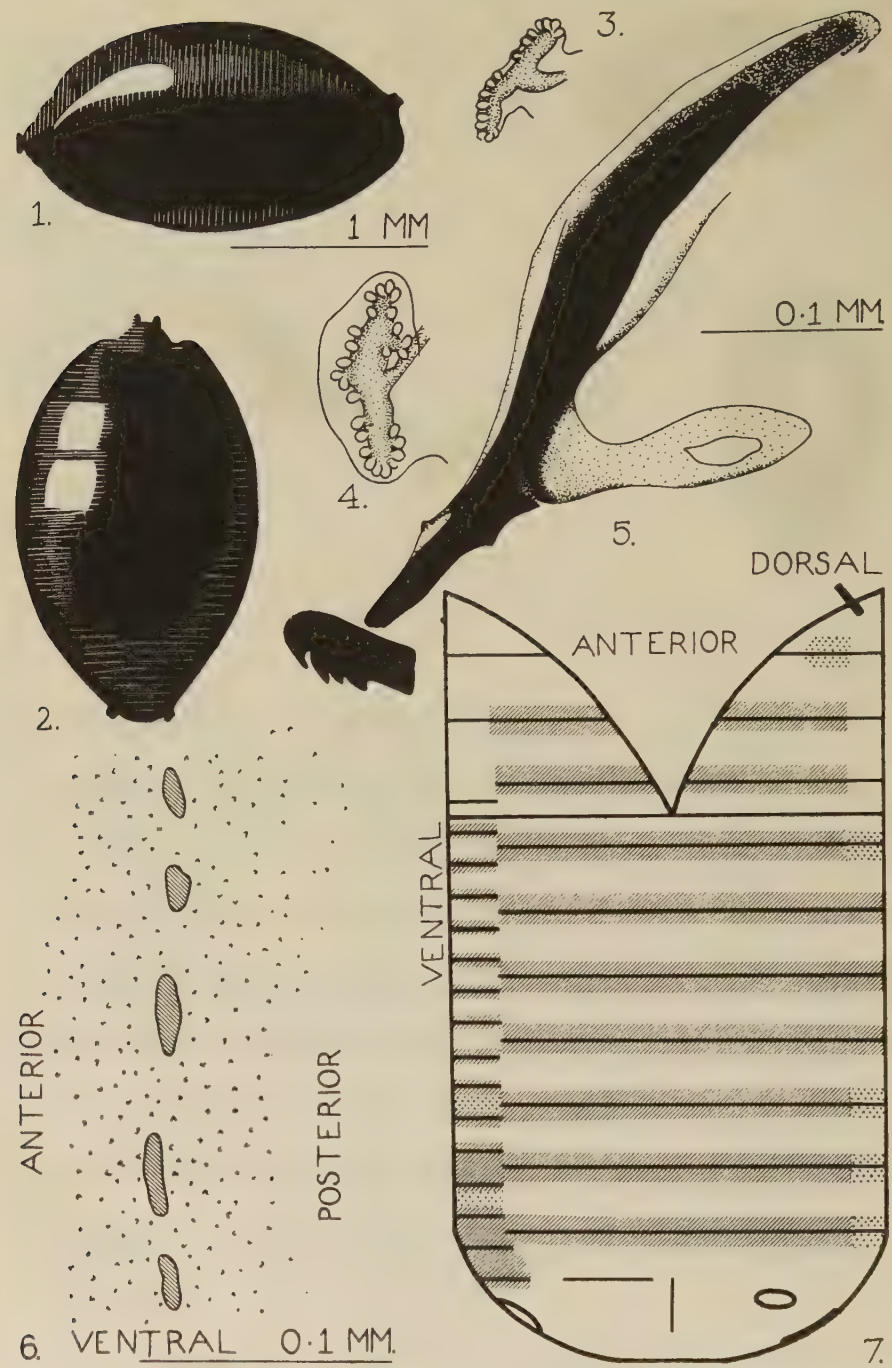


Fig. 6.—*P. obscurella* Fallén. (1) Side view of puparium. (2) Dorsal view of puparium. (3) Anterior spiracle of larva. (4) Posterior spiracle of larva. (5) Larval mouthparts, third instar. (6) Portion of post-fourth abdominal tubercle band. (7) Muscle scar and tubercle band pattern.

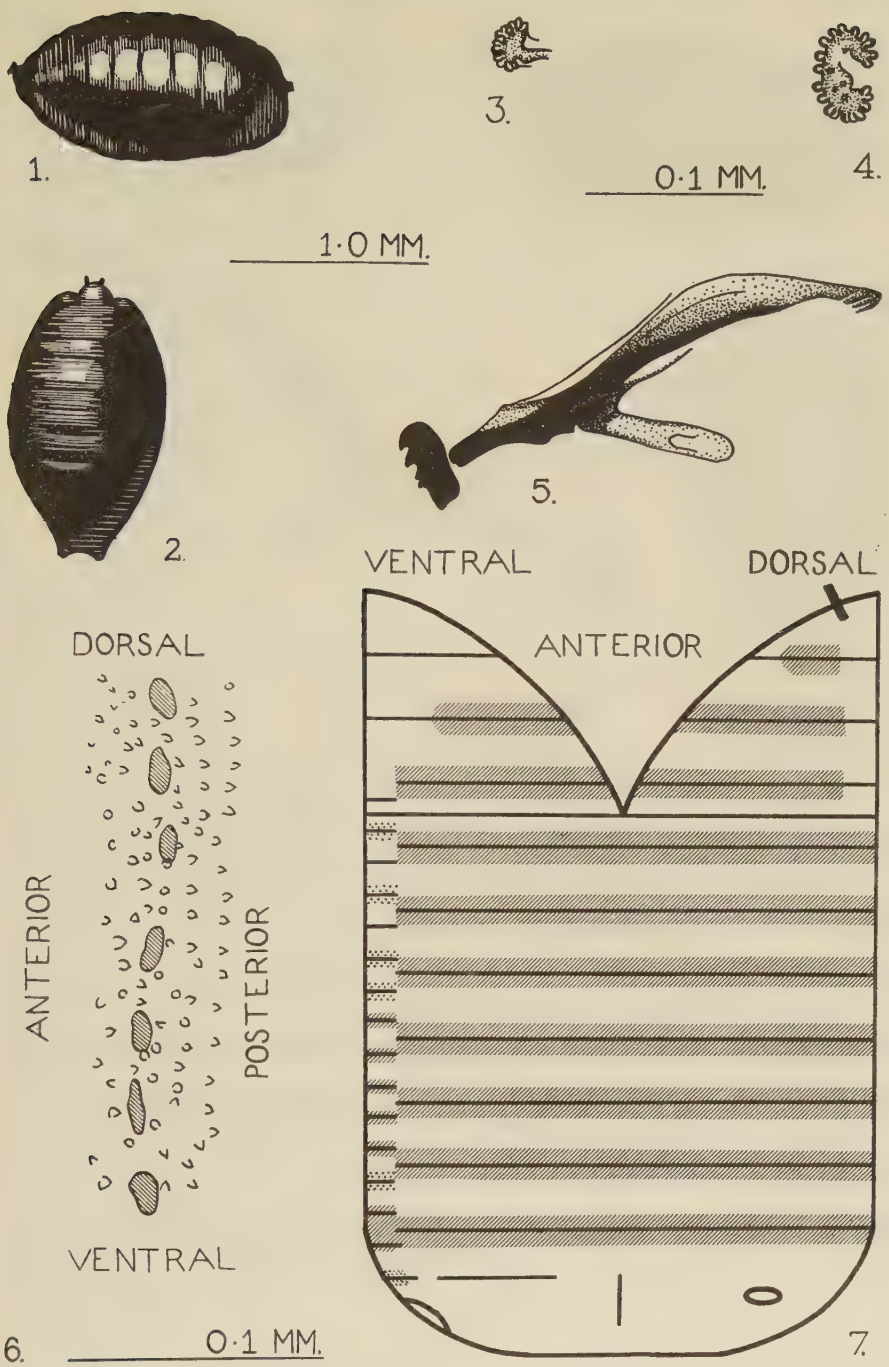


Fig. 7.—*P. silai* Hering. (1) Side view of puparium. (2) Dorsal view of puparium. (3) Anterior spiracle of larva. (4) Posterior spiracle of larva. (5) Larval mouth-parts, third instar. (6) Portion of post-fourth abdominal tubercle band. (7) Muscle scar and tubercle band pattern.

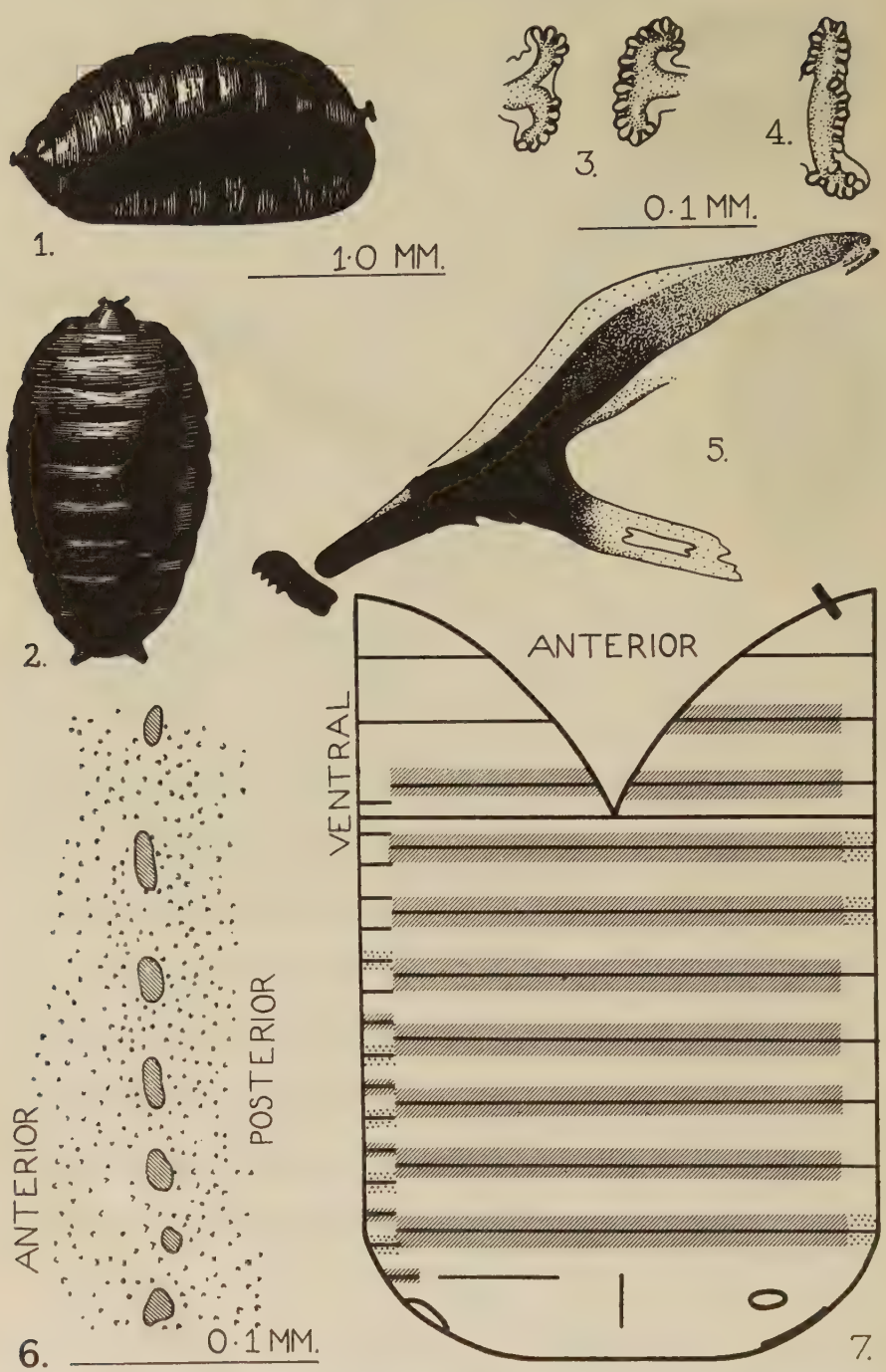


Fig. 8.—*P. spondylii* Robineau-Desvoidy. (1) Side view of puparium. (2) Dorsal view of puparium. (3) Anterior spiracles of larva. (4) Posterior spiracle of larva. (5) Larval mouthparts, third instar. (6) Portion of post-fourth abdominal tubercle band. (7) Muscle scar and tubercle band pattern.

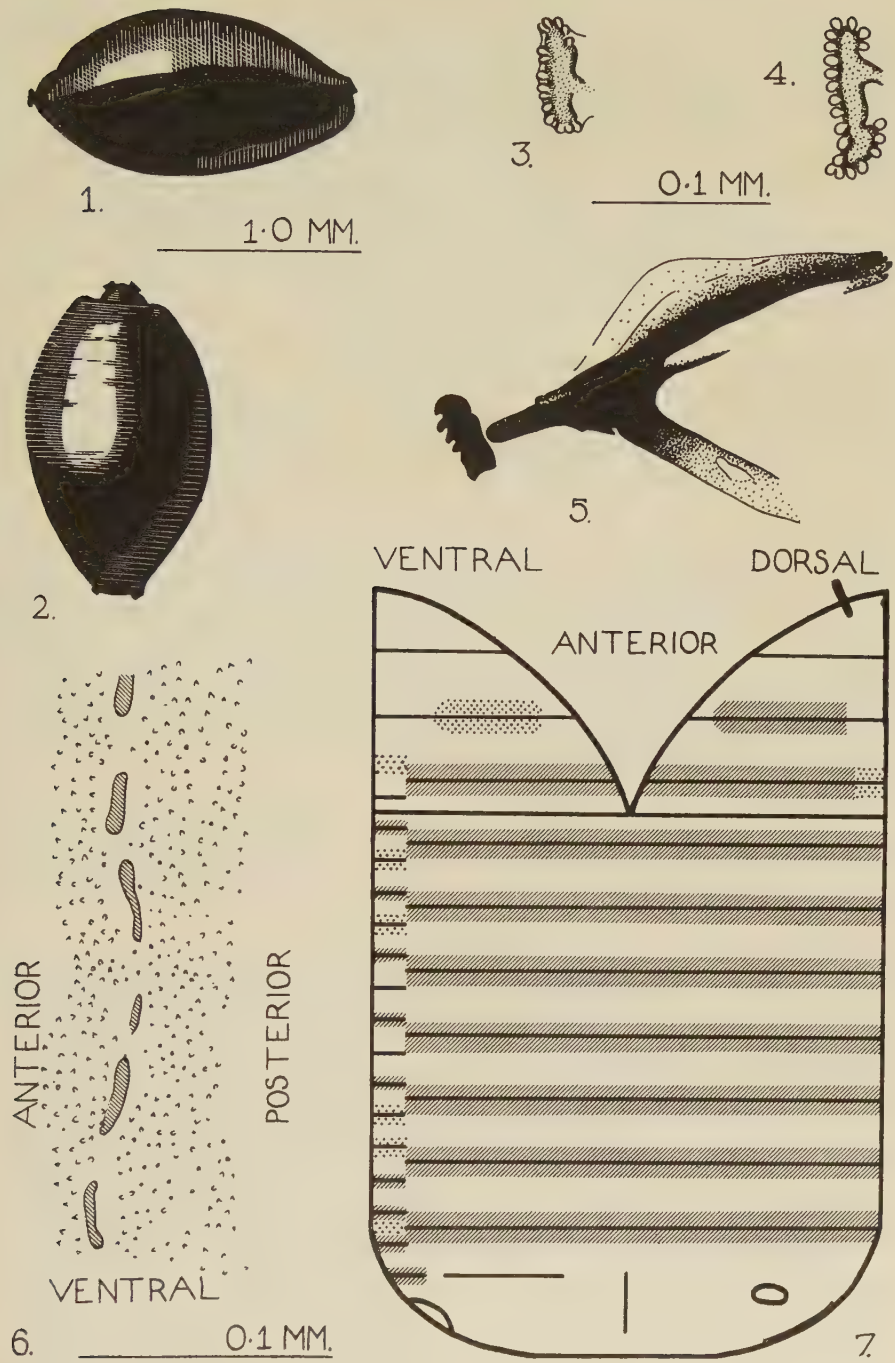


Fig. 9.—*P. tordylii* Hering. (1) Side view of puparium. (2) Dorsal view of puparium. (3) Anterior spiracle of larva. (4) Posterior spiracle of larva. (5) Larval mouth-parts, third instar. (6) Portion of post-fourth abdominal tubercle band. (7) Muscle scar and tubercle band pattern.

THE EFFECT OF SOCIAL FACILITATION ON THE OVARIAL DEVELOPMENT OF BUMBLE-BEE WORKERS.

By J. B. Free.

(*Bee Research Department, Rothamsted Experimental Station, Harpenden, Herts.*)

[Communicated by Professor O. W. Richards.]

Introduction.

Although the ovaries of worker bumble-bees normally remain rudimentary, they may develop under certain conditions and eggs may be laid. The behaviour of egg-laying workers has been investigated by Free (1955). In the present study different numbers of bumble-bees have been confined together in order to determine any effect of group stimulation on ovarial development.

Method.

Bumble-bee workers were captured whilst foraging. A proportion of them were dissected immediately on return to the laboratory and their ovarial development measured. The remainder were confined in small cages, each of which was provided with a solution of 50 per cent. sugar syrup and a ball of pollen approximately 10 mm. in diameter. The bees were divided into three sets which were kept at room temperature, 28° C. and 32° C. respectively. Each set contained bees which were confined singly, in pairs, in groups of five and in groups of ten.

After seven days the ovarial development of all the surviving bees was measured. The mean number of eggs in the ovarioles of a bee will be referred to as its ovarial index. The number of eggs that had been laid in each cage was also counted.

Results.

Forty *Bombus pratorum* and 16 *Bombus agrorum* foragers which were dissected on the day of their capture had mean ovarial indices of 2·8 and 2·0 respectively. The results obtained from the dissection of bees that had been confined in cages are given in Table I.

There is no significant difference between the ovarial development of bees which had been kept in equivalent numbers at 28° C. or at 32° C. There is, however, a highly significant difference between the ovarial development of bees kept at these temperatures and of those kept at room temperature in the case of *B. pratorum* workers kept in isolation and groups of two and five, and in the case of *B. agrorum* workers kept in isolation ($P < 0{\cdot}001$ for each comparison).

In general, the ovarial development of workers increased with the number of workers confined together. Considering the combined results obtained by keeping bees at 28° C. and 32° C., it is found that the ovaries of *B. pratorum* workers kept in groups of two were significantly larger than those kept in isolation ($P < 0{\cdot}02$) and, furthermore, workers confined in groups of five or ten possessed ovaries which had developed significantly more than those

TABLE I.—*The mean ovarial index of worker bumble-bees confined in groups of various sizes. The number of bees dissected is given in brackets. The error limits shown are the standard errors of the means.*

Number of workers confined together.	Temperature at which confined.		
	Room temp.	28° C.	32° C.
B. pratorum—			
1 . .	3·4±0·39 (33)	6·7±0·30 (16)	7·5±0·41 (6)
2 . .	5·4±0·49 (18)	8·6±0·46 (8)	7·7±0·59 (7)
5 . .	6·4±0·44 (19)	9·4±0·55 (7)	9·5±0·85 (10)
10 . .	8·3±0·59 (17)	10·3±0·89 (7)	9·4±0·46 (10)
B. agrorum—			
1 . .	3·0±0·21 (18)	5·0±0·33 (8)	5·7±0·44 (8)
2 . .	5·1±0·61 (6)	.	6·5±0·49 (9)
5 . .	7·2±0·89 (5)	7·0±0·39 (5)	7·5±0·39 (5)
10 . .	.	8·3±0·97 (9)	8·0±0·46 (10)

workers kept in groups of two ($P < 0{\cdot}02$). *B. agrorum* workers kept in groups of five or ten had significantly larger ovaries than workers that had been kept isolated ($P < 0{\cdot}001$). As well as possessing better-developed ovaries, the bees in the larger groups also tended to lay more eggs (Table II).

TABLE II.—*The mean number of eggs laid by worker bumble-bees confined in groups of various sizes.*

	Number of workers confined together.			
	1	2	5	10
B. pratorum workers . .	0·6	3·9	4·4	6·1
B. agrorum workers . .	0·9	1·9	2·4	2·4

DISCUSSION AND CONCLUSIONS.

It is apparent that the development of a worker's ovaries may be influenced both by temperature and by the number of other bees present. Since there is no marked difference between the ovarial development of bees kept in the larger groups at room temperature or at 28° C. and above, it appears that the retarding influence of low temperature on ovarial development may be compensated by the presence of sufficient bees, probably because the environmental temperature is raised with an increase in the number of bees present. However, the number of bees present also influences ovarial development when temperature is not a limiting factor.

The effects of social facilitation have been demonstrated in groups of animals of several different species. The presence of fellow members of the same species may result in the individuals feeding more as in the case of birds (Katzu and Révész, 1921), rats (Harlow, 1932) and fish (Welty, 1934), and in increased individual work as in the case of humans (Allport, 1924) and ants (Chen, 1938*a* and *b*).

A direct measurement of the amount of food eaten by bumble-bee workers in the present experiment would have been pointless since, in addition to the

food needed for individual metabolic requirements, an unknown part of the food was used for wax formation or to feed the brood. Since, however, ovarial development was greater in those workers kept in the larger groups, it is most probable that they had consumed more food than the workers kept in the smaller groups. But it is also possible that the workers kept in large groups tended to " cluster " together more, and were relatively less active than those in the smaller groups.

Hess (1942) found that worker honey-bees kept in isolation failed to develop their ovaries. Bumble-bee workers appear less dependent on the presence of fellow members of their own species than do honey-bee workers, since some of them even laid eggs whilst in solitary confinement.

In a natural bumble-bee colony the ovaries of some of the workers may develop at about the climax of the growth of the colony. Under these circumstances the temperature of the colony has become relatively stable at about 30° C. (Himmer, 1933), and the population is at its maximum. As shown above, both these factors may contribute towards the development of the ovaries of an individual worker.

Summary.

1. Within certain limits, the extent to which the ovaries of bumble-bee workers develop is increased with the number of workers kept together. However, even the ovaries of workers kept in isolation sometimes develop sufficiently for eggs to be laid.

2. It is suggested that these results can possibly be explained by differences in the amount of food consumed by workers belonging to groups of different sizes.

References.

Allport, F. H., 1924, *Social psychology.* Boston, Mass., U.S.A.

Chen, S. C., 1938*a*, Social modification of the activities of ants in nest building. *Physiol. Zool.* **10** : 420–36.

—— 1938*b*, The leaders and followers among the ants in nest building. *Ibid.* **10** : 437–55.

Free, J. B., 1955, The behaviour of egg-laying workers of bumble-bee colonies. *Brit. J. anim. Behav.* **3** : 147–53.

Harlow, H. F., 1932, Social facilitation of feeding in the albino rat. *J. Genet. Psychol.* **41** : 211–21.

Hess, G., 1942, Ueber den Einfluss der Weisellosigkeit und des Fruchtbarkeitsvitamins E auf die Ovarien der Bienenarbeiterin. *Beih. Schweiz. Bienenztg.* **1** : 33–109.

Himmer, A., 1933, Die Nestwärme bei *Bombus agrorum* F. *Biol. Zbl.* **53** : 270–6.

Katzu, D. and Révész, G., 1921, Experimentelle Studien zur vergleichenden psychologie (Versüche mit Hühnern). *Z. angew. Psychol.* **18** : 307–20.

Welty, J. C., 1934, Experiments on group behaviour of fishes. *Physiol. Zool.* **7** : 85–128.

OBSERVATIONS ON COLONIES OF HONEY-BEES SUBJECTED TO TREATMENTS DESIGNED TO INDUCE SWARMING.

By J. Simpson.

(*Bee Research Department, Rothamsted Experimental Station, Harpenden, Herts.*).

[Communicated by Professor O. W. Richards.]

Introduction.

Colonies of honey-bees are encouraged to swarm by lack of sufficient space in their hives (Huber, 1792). It has been suggested by Gerstung (1926) that swarm preparations can also be initiated by a surplus of brood food[1] resulting from the presence in the colony of more bees with active pharyngeal glands than are necessary to supply the food required by the larvae. The results of attempts to induce colonies to swarm by applying these two factors separately and in combination are described in the present paper.

Methods.

The following treatments were applied to colonies :

(1) The bees were overcrowded by reducing the size of the hives to 1 " brood chamber " (volume approx. 35 litres).

(2) All eggs and brood in the larval stage were removed from colonies, thus leaving the adult bees without the normal outlet for any brood food which they might secrete. The combs which contained eggs and larvae were removed at the beginning of the treatment and the eggs subsequently laid by the queens were removed at intervals of three days or less, *i.e.* before hatching. The eggs removed were transferred to other colonies and, from these, combs of pupal (sealed) brood were removed and transferred to the colonies from which the eggs had been taken, in order to maintain a supply of young bees in them.

(3) Colonies were given extra combs of eggs from which larvae hatched for the bees to feed. This treatment was complementary to (2). No prevailing theories or experience suggested that it would induce swarming, but in the absence of any real knowledge about the factors which encourage swarming it was thought worth while to observe its effects.

(4) Colonies were given additional pupal brood so that the resulting adults increased the proportion of young bees to the number of larvae requiring food. This treatment was not applied continuously ; each colony was given a number of combs containing pupal brood on a single occasion only.

[1] The food which the larvae receive probably contains material (mainly sugar) regurgitated from the honey-stomachs of the adult bees, though the pharyngeal glands supply most of the protein in it (Haydak, 1943 ; von Planta 1888, 1889 ; Simpson, 1955). The term " bee milk " has been used by Smith (1949) and others to distinguish the material secreted by the pharyngeal glands from the food actually given to the larvae.

Experiments and Results.

A. *Effects of the Treatments when Applied Singly.*

These preliminary trials were made in 1952 when sufficient colonies were not available for a controlled experiment. It was possible, however, to compare the behaviour of colonies under treatment at any given time with that of colonies not then being treated. The treatments were applied to colonies whose queens could fly (*i.e.* had not had their wings clipped) and no attempt was made to destroy any queen cells produced.

The colonies under treatment were generally examined every three to five days unless the application of the treatment required more frequent inspections, but occasionally longer periods elapsed between the inspections. All cases in which queen rearing was begun and then discontinued before the young queens had reached maturity were therefore not necessarily observed.[2] The colonies were housed in hives made up only of " brood chambers ", between which no queen excluders (slotted metal sheets through which worker bees, but not queens or drones, can pass) were used except when required to facilitate the separation of brood in its different stages. Care was taken that all colonies, except those which were being experimentally overcrowded, had a larger area of comb in their hives than the bees could occupy.

(1) *Crowding of Bees in the Hive.*

Three colonies (Nos. 1, 2 and 3) were crowded on 9th May. The space occupied by the bees before crowding was approximately $2\frac{1}{2}$ brood chambers by colony 1, $2\frac{1}{2}$ by colony 2 and $1\frac{1}{2}$ by colony 3. The treatment did not cause any of the bees to remain permanently outside their hives, but they did show a strong tendency to " flow " out over the sides when the roofs were removed for inspection and only returned slowly via the entrance after the disturbance had ceased. Crowding was discontinued on 2nd June after 24 days. By that date no queen cells[3] had been observed in colony 3, and the few produced by colonies 1 and 2 were destroyed by the bees before they reached maturity. Nectar was abundant during the period of treatment of these colonies and on this account the egg laying of the queens was greatly restricted by shortage of empty cells in the combs.

On 2nd June, the crowding treatment was applied to colonies 4, 5 and 6, which were very large as a result of additions of pupal brood on 9th May. Before crowding, the bees of colony 4 occupied 4 brood chambers, those of colony 5 occupied 3 and those of colony 6 occupied $2\frac{1}{2}$. The degree of overcrowding of colonies 4 and 5 was much greater than had been achieved with the colonies crowded in May. About a third of the bees in colony 4 were unable to enter the hive and formed a cluster at the entrance. Colony 5 swarmed on 17th June, colony 6 on 24th June and colony 4 on 27th June. All three colonies were still overcrowded with bees when swarming took place, but since there was a dearth of nectar during the period of crowding the egg laying of the queens had

[2] The times taken for three stages in the development of queen honey-bees are, approximately, as follows : Laying to hatching of eggs, 3 days ; hatching of egg to sealing of cell (larval stage), 5 days ; sealing of cell to emergence of adult (pupal stage), 7 days.

[3] Throughout this paper reference to " queen cells " indicates only those occupied by eggs, larvae, or pupae.

not been restricted by lack of cell space. The queen of colony 4 showed no obvious diminution in her egg output before swarming. The bees of this colony destroyed their queen cells twice in the larval stage and once in the pupal stage, and finally swarmed when the only queen cell present contained an egg.

On 12th August the crowding treatment was applied to colony 27, previously increased in size by the addition of pupal brood and then occupying about $2\frac{1}{2}$ brood chambers. This colony was crowded for 16 days but was not seen to make any swarm preparations.

(2) *Removal of Eggs and Larval Brood.*

This treatment was applied to colony 9 from 9th May for 45 days, to colony 1 from 10th June for 13 days and to colony 2 from 9th June for 14 days. All three colonies showed transient production of queen cells but nothing more. The treatment was also applied from 16th July for 16 days to colony 7 which had a queen of the current year, and from 12th August for 21 days to colony 4 which had by then acquired a new queen reared in the current season. Neither of these colonies was observed to produce any queen cells under treatment.

Although this treatment did not cause the colonies to swarm, there was some evidence that it produced a surplus of brood food in the colonies. When (as happened occasionally) a few eggs which should have been removed were overlooked, the larvae which hatched were seen to be floating on the top of large masses of brood food which sometimes extended almost to the mouths of their cells ; the larvae normally lie in small pools of food in the bases of the cells. This, moreover, continued throughout the feeding life of the larvae, whereas in normal colonies food is not readily visible in cells containing larvae more than about three days old. The presence of this superabundance of food did not indicate that the larvae were being reared as queens, as there was no sign of structural conversion of worker cells into queen cells. The queens in colonies under this treatment always appeared to be laying with particular vigour and showed no sign of that reduction in the rate of laying which is frequently associated with swarming. The brood food surplus appeared to continue and possibly to increase throughout the periods of treatment and was not merely a temporary consequence of the sudden removal of larval brood.

(3) *Addition of Eggs.*

Colony 10 received additional eggs for 45 days from 9th May, for 16 days from 16th July and for 21 days from 12th August. Colony 8 did so for 13 days from 10th June, for 16 days from 16th July and for 21 days from 12th August. Neither of these colonies swarmed and preparations to do so were not observed during the irregular inspections made.

In contrast to the effect of egg removal, addition of eggs to colonies appeared to produce signs of an insufficiency of brood food. Often no food was visible in the cells, even in those containing very young larvae. Many larvae appeared to be dying of starvation.

(4) *Addition of Pupal Brood.*

On 9th May large quantities of pupal brood, taken from non-experimental colonies, were added to colonies 4, 5 and 6. Colonies 4 and 5 each received

22 combs containing brood and colony 6 received 11 combs. It was estimated that this treatment increased the amounts of pupal brood by at least three times in colonies 4 and 5 and one and a half times in colony 6. Each colony was given an extra chamber containing empty combs to ensure that no crowding was produced by the emergence of young bees. Although by about 22nd May all this extra brood had emerged and the colonies had greatly increased in size, by 2nd June colony 5 had produced no queen cells and colonies 4 and 6 had done so only transiently.

On 2nd June colony 3, which had previously failed to swarm when subjected to overcrowding, was given 20 combs containing pupal brood. On 10th June it had queen cells in all stages of development, but on 13th June these had apparently all disappeared. However, on 25th June the original queen was found to have been replaced by a young one which had probably emerged from a cell which had been overlooked at previous inspections. Since there was no visible diminution in the number of bees present it was unlikely that the colony had swarmed.

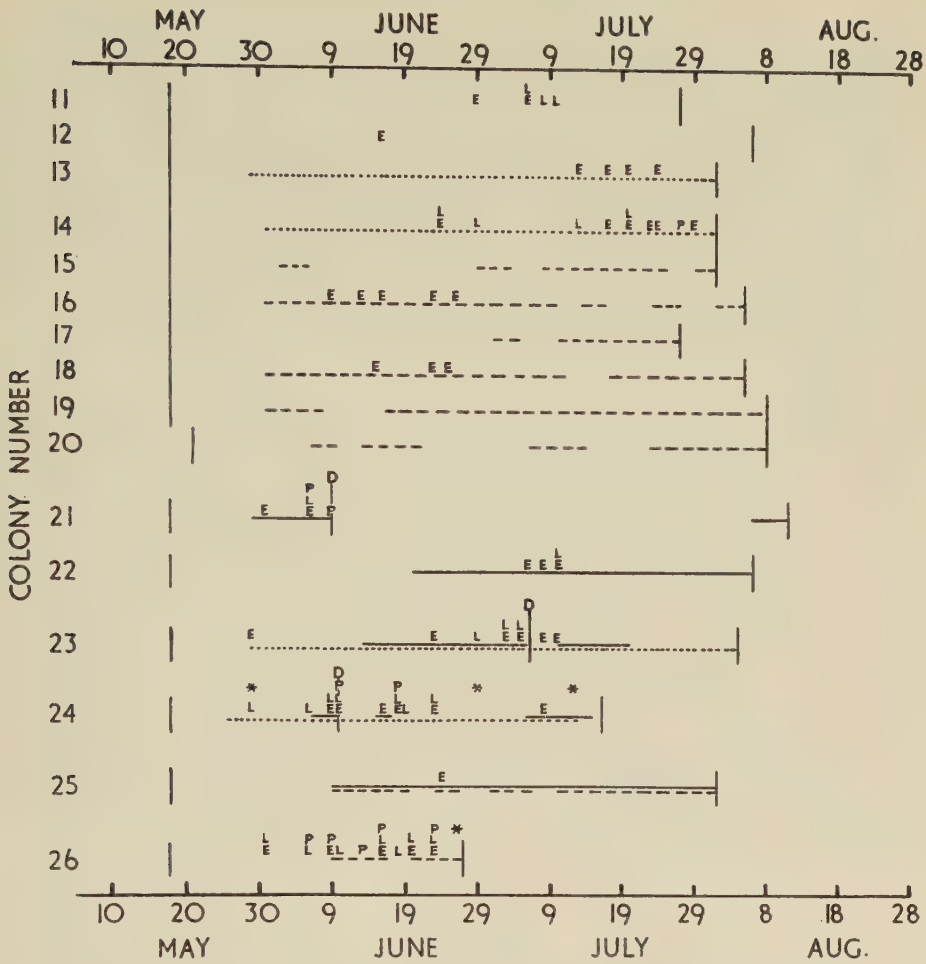
Colony 27, which had previously been too small for experiment, was given 16 combs containing pupal brood on 25th June. By 12th August when it was subjected to overcrowding, it had not swarmed nor had any queen cells been observed.

No signs of surplus brood food were found in any of the colonies given this treatment, nor was there any visible evidence of that congestion of adult bees in the brood nest which Demuth (1921) considers to be produced by an excess of young bees. The proportion of bees to brood was not, of course, nearly so great as with treatment (2) where the only larvae present were a few left by accident.

B. *The Interaction of Crowding and Deprivation of Larval Brood.*

In the experiment carried out in 1953, colonies were subjected in pairs to each of the following treatments : removal of eggs (13 and 14) ; crowding (21 and 22) ; removal of eggs and crowding (23 and 24) ; addition of eggs and crowding (25 and 26). Six (15–20) colonies were given addition of eggs only and two (11 and 12) colonies remained untreated. The methods of management and frequency of observations were similar to those in 1952, except that sealed queen cells were removed whenever found, and colonies were divided whenever they reached a stage where beekeeping experience suggested that they were likely to swarm. The periods of treatment and the behaviour of the colonies is shown in figure 1.

Because of their small size some colonies were not effectively crowded at the beginning of the experiment by the reduction of their hives to single brood chambers, but only became crowded after a period of growth. One colony (No. 26) failed to become crowded at all, and those colonies which were divided took some time afterwards to recover their strength sufficiently to become crowded. In no case was the degree of crowding as great as that achieved with the colonies treated in 1952. Removal of eggs from colony 24 was discontinued after the third disappearance of its queen, otherwise this treatment was applied continuously from the end of May to the end of July—a period of about 60 days.



KEY–FINDINGS

E QUEEN CELLS WITH EGGS
L QUEEN CELLS WITH LARVAE
P QUEEN CELLS WITH PUPAE

VERTICAL LINES MARK THE BEGINNING AND END OF THE OBSERVATIONS

KEY–COLONY TREATMENTS

——— PERIOD OF CROWDING
– – – – PERIOD OF ADDITION OF EGGS
····· PERIOD OF REMOVAL OF EGGS
* QUEEN DISAPPEARED–NEW QUEEN GIVEN
D COLONY REDUCED IN STRENGTH AS SWARMING WAS THOUGHT LIKELY

FIG. 1.—Observations of queen cells and probable preparations for swarming in the colonies receiving various treatments in 1953.

Addition of eggs to colonies could not be continuous since it was desired to avoid the deterioration which had occurred in colonies given this treatment in 1952. Eggs were only given to colonies when the larvae they already had were not being neglected. The periods of treatment shown in figure 1 are those during which the larvae from the added eggs would require to be fed. In spite of this precaution many eggs apparently failed to produce adult bees since the colonies given this treatment increased in size less rapidly than did the other colonies.

None of the treatments were invariably followed by actual or potential swarming, nor, on the other hand, did any treatment entirely prevent the production of queen cells. In colony 26 it was noted that queen larvae were being fed, apparently adequately, while worker larvae were starving, thus showing that an extreme shortage of brood food does not necessarily prevent the rearing of queens.

The three colonies which reached a condition in which swarming was judged to be imminent were all receiving treatments which included crowding. Factorial analysis of the numbers of those colonies which appeared likely to swarm, those which produced queen cells but did not swarm or appear likely to do so, and those which did not produce queen cells, showed ($P < 0{\cdot}02$) that, in spite of its low intensity, crowding probably did increase the tendency of colonies to swarm, but failed to show any effect of the treatments involving transfer of eggs.

Samples of at least 100 of the bees which were clustering on the combs were taken from each colony on 15th July, about six weeks after treatment was begun. Twenty bees in each sample were dissected and their pharyngeal glands examined. No significant differences were found between the treatment groups and in every sample, including those from colonies which had no brood to feed, the pharnygeal glands of more than half of the bees showed the degree of enlargement (Maurizio, 1954) which is associated with secretion of " bee milk."

Discussion.

The observation that a surplus of brood food can occur in colonies of honey-bees shows that the adaptability of the worker bees to the requirements of their colony (Rösch, 1930) is not complete and that, independently of any stimulus which they may receive from hungry larvae, they have some inherent tendency either to produce brood food at a particular period in their adult life or to continue doing so when once they have begun. The latter explanation seems improbable since the average length of life of bees in normal colonies in the summer has been found to be under five weeks (Ribbands, 1953), whereas brood food surplus when eggs were being removed was observed to continue for at least 45 days. The data obtained are insufficient to exclude the possibility that the availability of brood food in colonies does have some slight influence on their tendency to swarm ; it is even possible (since both colonies which received the double treatment did show an apparent readiness to swarm) that overcrowding may invariably produce swarming when it occurs in colonies with surplus brood food. The apparent induction of swarming by the removal of larval brood from colonies by Perepelova (1928) may perhaps be explained by some such combination of effects. It is clear, however, that brood food

surplus alone is not sufficient to induce swarming, and also that, at least under certain conditions, queen cells can be reared in colonies with a deficiency of brood food.

Colonies which have their queens removed usually begin to rear new queens within a few hours. This behaviour must be directly due to removal of the queen and not to brood food surplus, since the number of larvae to be fed cannot diminish until three days after the queen has been removed. Butler (1954) has shown that queen rearing is inhibited by a substance which the worker bees of a colony lick from the surface of their queen's body. The immediate cause of queen rearing during swarm preparations is presumably absence or ineffectiveness of this inhibiting substance but it has yet to be shown whether this is a cause or a consequence of the swarm preparations.

The failure of some colonies to swarm under the extreme conditions of crowding produced in 1952 would appear to indicate that crowding only induces swarming if certain other conditions are fulfilled. It may be noted that these failures were outside the period of the year (June and July) in which beekeepers' records (Simpson, 1957) show that queen cells most frequently occur.

It can be seen from figure 1 that colonies which began to rear queens often ceased to do so of their own accord, destroying the young queens as eggs, larvae or pupae. In the 1953 experiment it was found that queen cells were destroyed by the bees on 24 occasions at the egg stage or later, and on 12 occasions when they had reached the larval stage at least. In the 1952 observations, where pupae were not destroyed by the observer when seen, young queens were known to have reached the egg stage on six occasions, the larval stage on eleven occasions and the pupal stage on three occasions, before their destruction by the adult bees. It is thus apparent that when a colony in which a laying queen is present is seen to be rearing young queens, this by no means always indicates that if undisturbed it will swarm or even rear the queens to maturity ; the frequency and thoroughness with which colonies are inspected in beekeeping practice may therefore influence judgment of the proportion which are likely to swarm.

The emergence of swarms from three colonies at a time when they had many empty cells in their combs disproves the conclusion of Lindauer (1955) that the stimulus which leads to the actual emergence of a swarm is inability of foraging bees to get rid of loads of nectar because of absence of empty cells to contain them. However, since foraging honey bees do not normally discharge nectar directly into cells, Lindauer's results may perhaps be better explained by assuming that in a colony which is making preparations to swarm the house bees cease to accept nectar from the foragers.

Summary.

1. Attempts were made to induce colonies of honey-bees to swarm by crowding the bees in the hive, depriving them of larval brood, giving them extra larval brood or extra pupal brood, and by combination of the first two treatments.

2. Evidence of shortage of brood food was observed in those colonies which received additional larval brood. Evidence of brood food surplus was observed in those which were deprived of larval brood.

3. Under conditions of brood food deficiency queen larvae in one colony were fed, apparently quite adequately, even when worker larvae were being neglected.

4. Swarming, when colonies were crowded, was found to be possible under conditions where the queens of the colonies had plenty of empty cells in which to lay eggs and in which the queen of one colony, at least, was still laying freely.

5. None of the treatments, except crowding plus removal of eggs, which was only applied to two colonies, were invariably followed by swarming.

6. It is concluded that brood food surplus is probably not essential for the commencement of swarm preparations and when acting alone is insufficient to cause such preparations.

7. Colonies which began rearing young queens frequently destroyed them, sometimes even in the pupal stage; the onset of queen rearing in a colony did not necessarily indicate that it would swarm or even rear the queens to maturity.

References.

Butler, C. G., 1954, The method and importance of the recognition by a colony of honey-bees (*A. mellifera*) of the presence of its queen. *Trans R. ent. Soc. Lond.* **105** : 11–19.

Demuth, G. S., 1921, Swarm control. *Fmrs. Bull. U.S. Dep. Agric.* **1198** : 1–28.

Gerstung, F., 1926, *Die Biene und seine Zucht.* 7th ed. Berliu.

Haydak, M. H., 1943, Larval food and development of castes in the honey-bee. *J. econ. Ent.* **36** : 778–92.

Huber, F., 1792, *Nouvelles observations sur les abeilles I.* (*New observations on bees*). (Transl. 1926). Hamilton, Ill.

Lindauer, M., 1955, Schwarmbienen auf Wohnungsuche. *Z. vergl. Physiol.* **37** : 263–324.

Maurizio, A., 1954, Pollenernährung und Lebensvorgänge bei der Honigbiene (*Apis mellifica* L.). *Landw. Jb. Schweiz.* **68** : 115–82.

Perepelova, L. I., 1928, Laying workers, the egg-laying activity of the queen and swarming. (In Russian). *Opuit. pas.* : 214–7.

Planta, A. von., 1888, Sur la patée nutritive des Abeilles. *Zeit. Phys. Chem.* **12** : 327.

——, 1889, Ueber den Futtersaft der Bienen. *Hoppe Seyl. Z.* **12** : 324–54.

Ribbands, C. R., 1953, *The behaviour and social life of honey-bees.* London.

Rösch, G. A., 1930, Untersuchungen über die Arbeitsteilung im Bienenstaat. 2. Die Tätigkeiten der Arbeitsbienen unter experimentell veränderten Bedingungen. *Z. vergl. Physiol.* **12** : 1–71.

Simpson, J., 1955, The significance of the presence of pollen in the food of worker larvae of the honey-bee. *Quart. J. micr. Sci.* **96** : 117–20.

—— 1957, The incidence of swarming among colonies of honey-bees in England. *J. agric. Sci.* (in press).

Smith, J., 1949, *Better queens.* Fort Myers, Florida.

ON THE HABITS AND LIFE HISTORY OF CAPTIVE EMESINE BUGS (HEMIPTERA : REDUVIIDAE).

By J. D. Gillett.

(*East African Virus Research Institute, Entebbe, Uganda*).

A species of Emesine bug, *Bagauda gilletti* Miller, has recently been used in this laboratory in tests on the maintenance of yellow fever virus in arthropods which prey on mosquitoes (Gillett, *in press*). The bugs, which were caught near Entebbe, were found to be an undescribed species, but have since been named by Miller (1956). As little seems to be known about the habits and life history of this subfamily of strange insects, it was considered worth while to record briefly some observations which were made in the course of the work mentioned above.

Activity.

Adult males and females were taken on the buttress trunk of a tree in Zika forest about eight miles from Entebbe. Each was found resting flush against the tree trunk, motionless, with its thorax and abdomen in contact with the tree. On being disturbed they raised themselves on their mid- and hind legs and either walked over the surface of the tree, with the folded raptorial fore legs held out in front, or sprang up and down on their long legs in the way characteristic of Tipulids. If disturbed no more, they soon resumed the position of rest, but further disturbance resulted in their dropping off the tree trunk to the ground.

Some of the bugs were collected alive in glass tubes and taken to the laboratory, where each was placed separately in a small Barraud's cage (*c.* 13 cm. square) and kept at 25° C. and 70 per cent. R.H. In these cages the bugs also remained at rest during the day. At night, however, they could be seen wandering over the inner surfaces of their cages. Those that were not walking about were nevertheless active ; they were raised up on their extremely long, slender mid- and hind legs, with their long geniculate antennae executing movements over a wide area in front of them, similar to those described in the South American kissing bug, *Rhodnius prolixus* Stål, by Wigglesworth and Gillett (1934). After a few days' captivity some of them lost this nocturnal rhythm of activity and wandered at all hours. The difference between the state of rest, or akinesis, and awakening is very similar to that described in the bed bug, *Cimex lectularius* L., by Rivnay (1932) and in *R. prolixus* by Wigglesworth and Gillett (1934).

Walking.

In effect, these bugs are four-legged, as the raptorial fore legs take no part whatever in locomotion. Movement of the legs is usually slow, but, nevertheless, the bugs are at times able to move rapidly from one place to another because of the great stride made possible by the length of the mid- and hind legs, the femora and tibiae of which are together 44 and 60 mm. long respectively. They usually walk in a zig-zag path, taking a few steps in one direction, followed

by a few more in another. At times these bugs adopt a hesitant gait, the whole body swaying backwards and forwards two or three times between each step.

Feeding.

Each bug in its cage was supplied with live mosquitoes as food (*Aëdes* (*Stegomyia*) *aegypti* (L) and *A.* (*S.*) *africanus* Theo.). When in the awakened state, either standing still or walking, the very long (35 mm.) geniculate antennae sweep a wide area in front of them. If the bug is walking in its characteristic zig-zag manner, the path swept by the tips of the antennae is even wider and may be as much as 120 mm. Should the fine tip of one antenna make contact with a resting mosquito, the other antenna is immediately brought across and the mosquito is gently stroked by the tips of both antennae. The mosquito is not usually disturbed by this process, possibly owing to the excessive fineness of the tip of each antenna. After about five seconds the bug raises its raptorial fore legs above its head and darts them forward to capture the mosquito, which is drawn towards the bug's mouthparts and is sucked dry in the course of the next 20–40 minutes.

This brief description of the capture of prey by the bug is an oversimplification as, even when its position has been located by antennal contact, rarely is it in range for the catching mechanism to operate. The prey may be too near or too far from the bug, or out of line with its long axis, either in the horizontal or vertical planes. These difficulties are overcome by movements of adjustment which the bug makes soon after antennal contact has been established. The bug pivots round horizontally on its legs until the prey is directly ahead ; it then " leans " forwards or backwards to bring the prey to the right distance, and adjusts its level before raising the raptorial fore legs in preparation for the kill. All these adjustments are made without any movement of the tarsi in relation to the substratum, and are made possible by the great length of the femora and tibiae, which allow the body not only to pivot horizontally through about 60° but to move forwards and backwards through about 10 mm., or to be raised and lowered through about 10 mm.

These bugs are easy to keep in captivity ; adults have been maintained on a diet of two mosquitoes a day for over four months. On the other hand, as many as 24 mosquitoes may be caught and sucked dry by a single bug in a single day.

Life History.

Eggs, which were laid attached to the netting sides of the cages, are elongated in shape and dull brown in colour, the chorion being roughened by numerous tubercles. The operculum is white with a serrated margin. The eggs hatched in two to three weeks, the first stage nymphs having a very short telescoped abdomen, which is carried turned up almost over the thorax, in a way similar to that of certain immature mantids.

As these bugs were kept mainly to test their capacity to retain and multiply yellow fever virus after ingestion of infected mosquitoes, it was considered that they should be given the chance to feed on mosquitoes from their earliest days. Attempts at feeding the early stage nymphs on *A. aegypti* and *A. africanus* failed ; if the tip of one antenna came into contact with one of these mosquitoes

the bug would turn away from the mosquito and move off in the opposite direction. They would, however, feed readily on a very small species of mosquito, *Hodgesia cyptopus* Theo., the response being similar to that of adult bugs with larger mosquitoes. With three to four *Hodgesia* per bug per day, the nymphal stages lasted about two weeks. Not until the fifth or final nymph stage did larger mosquitoes elicit the catching response. This difference in response of the bugs when confronted with mosquitoes of different sizes recalls similar behaviour in the frog ; relatively small moving objects elicit the well-known catching and feeding response, whereas relatively large moving objects elicit an escape or fright response.

General Notes.

Animals that lie in wait and effect capture of their prey by means of some special apparatus would seem to require a wide field of perception. It is interesting to see how this is achieved in unrelated animals with similar habits. In the chameleon, for example, a wide field of vision is provided by the movements of the independently swivelling eye-turrets. Much the same result is achieved in the praying mantis by the extreme mobility of the head on its slender neck. In *B. gilletti* a very wide tactile field is provided by the independent movements of the two long antennae and by the great freedom of bodily movement afforded by the very long slender legs. It is interesting to note, also, that all three of these unrelated, relatively slow moving animals, at times adopt the same peculiar hesitant gait referred to above.

Summary.

Notes are recorded on some of the habits of an Emesine bug, particularly those concerned with walking and feeding.

References.

Gillett, J. D., *in press*, Laboratory tests on the maintenance of yellow fever virus in certain predatory arthropods. *Trans. R. Soc. trop. Med. Hyg.*

Miller, N. C. E., 1956, A new species of Emesinae (Hemiptera-Heteroptera : Reduviidae). *Proc. R. ent. Soc. Lond.* (B) **25** : 53–54.

Rivnay, E., 1932, Studies in tropisms of the bed bug *Cimex lectularius* L. *Parasitology* **24** : 121–36.

Wigglesworth, V. B. and Gillett, J. D., 1934, The function of the antennae in *Rhodnius prolixus* (Hemiptera) and the mechanism of orientation to the host. *J. exp. Biol.* **11** : 120–39.

Book Notices.

The Lepidoptera of Iraq. By E. P. Wiltshire. Rev. and enlged. 8vo. London (Kaye), 1957. Pp. [vi] + 162, 17 pls. Price 45*s*.

This work forms the first publication in a new series of surveys undertaken by the Iraq Ministry of Agriculture, of the fauna of that country, and is a second edition of Bulletin No. 30, published by the Ministry in 1944 and now out of print.

This edition is enlarged and revised. The introduction describes the plan and scope of the work, with an explanation of the systematic order followed and of ecological, phenological and zoogeographical terms used. The general conditions governing insect life in Iraq are also outlined.

The main body of the text comprises an annotated list of the 939 species of butterfly and moth known to occur in Iraq, giving under each species notes on its distribution, food-plant and phenology and its range outside Iraq. Harmful pests are indicated, as also are those which are known to attack cultivated plants or trees but have not yet been recorded as causing serious economic damage.

Four new species and six new subspecies are described. A list of references, a specific index and a list of pests arranged according to hosts complete thework.

A General Textbook of Entomology. By A. D. Imms. 9th ed. revised by O. W. Richards and R. G. Davies. 4to. London (Methuen), 1957. Pp. x + 886, text illust. Price 75*s*.

The new edition of this work, of which the last full edition appeared in 1934, retains the general plan of the original text-book, but every chapter has been extensively revised and the whole work expanded by about a quarter.

Most of the physiological sections in Part I have been rewritten to incorporate the advances made in the last twenty-five years.

The chapters dealing with systematic entomology have also been revised in almost all groups to meet the developments of modern taxonomic work and practice. New keys for the identification of families are included and the nomenclature brought up to date.

The numerous bibliographical references have all been collected, standardised and presented in a fuller and more useful form than in the original work.

Fifty new illustrations are included. A detailed 54-page index, which includes considerable synonymy, completes the work.

INDEX